Oological Record of Dinosaurs in South-Central Pyrenees (SW Europe):

Parataxonomy, diversity and biostratigraphical implications

Albert Garcia Sellés

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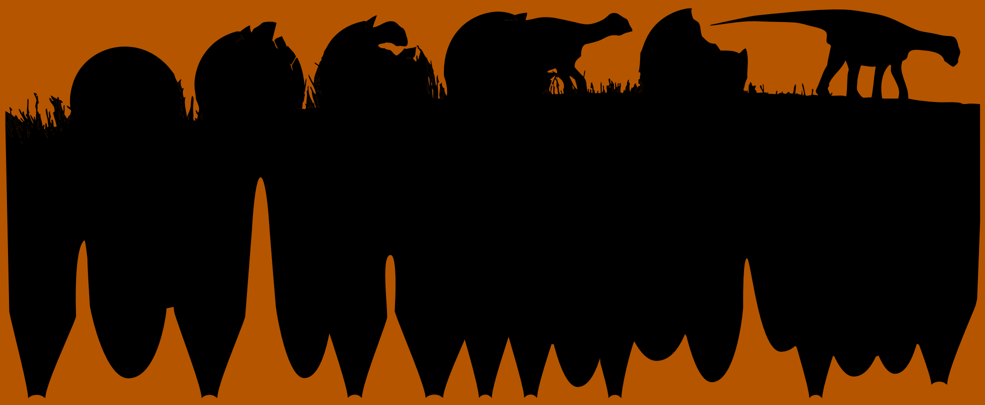
OOLOGICAL RECORD OF DINOSAURS IN SOUTH-CENTRAL PYRENEES (SW EUROPE):

PARATAXONOMY, DIVERSITY AND BIOSTRATIGRAPHICAL IMPLICATIONS



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2012

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OOLOGICAL RECORD OF DINOSAURS IN SOUTH-CENTRAL PYRENEES (SW EUROPE):

PARATAXONOMY, DIVERSITY AND BIOSTRATIGRAPHICAL IMPLICATIONS

Memòria presentada per **Albert Garcia Sellés** per optar al Grau de Doctor en
Ciències de la Terra per la Universitat de Barcelona,
sota la direcció del **Dr. Àngel Galobart Lorente**, Cap del Grup de Recerca del Mesozoic del
Institut Català de Paleontologia Miquel Crusafont
amb la tutela del **Dr. Xavier Dalclòs Martínez**, Professor titular del Departament d'Estratigrafia,
Paleontologia i Geociències Marines de la Universitat de Barcelona

Als meus pares;

“...Lightly on the knee she settles,
finds a nesting-place befitting,
where to lay her eggs in safety.
here she builds her humble dwelling,
lays her eggs within, at pleasure,
six, the golden eggs she lays there,
then a seventh, an egg of iron;
sits upon her eggs to hatch them...

...Quick the maiden moves her shoulders,
shakes her members in succession,
shakes the nest from its foundation,
and the eggs fall into ocean,
dash in pieces on the bottom...

...From one half the egg, the lower,
grows the nether vault of Terra:
from the upper half remaining,
grows the upper vault of Heaven;
from the white part come the moonbeams,
from the yellow part the sunshine,
from the motley part the starlight,
from the dark part grows the cloudage...”

The Kalevala. Rune I - Birth of Wainamoinen

Translated by John Martin Crawford (1888)

CONTENT

Acknowledgements (in Catalan)

Sens dubte aquesta és la part més esperada i llegida de qualsevol tesi doctoral, on tothom espera veure-s'hi reflexat o on trobar-hi anècdotes divertides. Però el protocol marca les normes, així que començarem per la part formal:

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troba representada en l'interior de la tesi.

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RESUME

RESUME (in Catalan)

La present tesi doctoral es centra en l'estudi de les restes oològiques atribuïdes a dinosaures del Cretaci superior de la zona del Prepirineu català, la seva sistemàtica, diversitat i implicacions taxonòmiques i biostratigràfiques.

MOTIVACIÓ, PROBLEMÀTICA I OBJECTIUS

Els dinosaures han fascinat a la humanitat des que la primera reconstrucció d'*Iguanodon* realitzada per W. Hawkins, l'any 1852, va despertar un gran interès, tant a nivell científic com a nivell popular en la societat victoriana. Però aquest interès no arriba de forma uniforme arreu. Els primers descobriments de restes fòssils de dinosaures al Pirineu central no es fan fins el primer quart del segle XX, i no és fins a mitjans dels anys cinquanta quan es posa de manifest la importància i la riquesa dels jaciments paleontològics de dinosaures de Catalunya. Gairebé cinquanta anys més tard, l'estudi dels dinosaures, i el seu entorn, és una disciplina fortament arrelada en la comunitat científica catalana. En aquest sentit, els estudis actuals sobre els darrers milions d'anys de l'era mesozoica no es centren únicament en l'estudi sistemàtic de les faunes de dinosaures, sinó que tenen per objectiu la reconstrucció i comprensió dels ecosistemes del Cretaci superior. És per aquest motiu que geòlegs i paleontòlegs del Institut Català de Paleontologia Miquel Crusafont (ICP), de la Universitat de Barcelona (UB) i de la Universitat Autònoma de Barcelona (UAB) han unit esforços per tal de d'incrementar el coneixement sobre la fauna, flora i els ecosistemes de fa més de 65 milions d'anys de la zona del Prepirineu català.

El present projecte de tesi aporta noves dades i nova informació sobre un registre fòssil que històricament ha estat poc estudiat. Els dinosaures, com a membres de la clade dels rèptils, eren animals amniotes i que es reproduïen mitjançant ous. L'estudi de la paleobiologia dels diversos components d'aquest grup, demostra que eren, majoritàriament, animals ovípars, i les restes de postes, nius i ous aïllats s'han preservat com a fòssils fins als nostres dies. Actualment, el registre oològic de dinosaures del Prepirineu es visualitza com un dels més importants a nivell mundial i pot proporcionar informació rellevant sobre la diversitat, la paleobiologia i la sistemàtica dels darrers dinosaures que varen viure i que han quedat registrats en els jaciments paleontològics d'Europa.

Malgrat la quantitat i diversitat de les restes d'ous i closques atribuïdes a dinosaures del Prepirineu, les restes del tipus *Megaloolithus*, associades a dinosaures sauròpodes, són les més abundants, representant més del 90% d'aquest registre fòssil. De fet, els ous megaloolítids són el tipus d'ou de dinosaure els més comú en el Cretaci superior a nivell mundial (Mikhailov, 1997; Carpenter, 1999). Degut a aquesta condició, s'han realitzat nombrosos estudis sobre la sistemàtica i diversitat d'aquest grup, sobre tot en base a fòssils d'una cronologia propera a la fi del Mesozoic. En estudis publicats a finals del segle passat, la oofamília Megaloolithidae contava amb 3 oogèneres i 24 ooespècies, distribuïdes per Sud Amèrica, Índia i Europa (Vianey-Liaud *et al.*, 1987, 1994; Calvo et a*l.*, 1997, entre d'altres), tot i que alguns autors apuntaven a una gran semblança entre alguns ootaxons. Estudis posteriors (Vianey-Liaud *et al.*, 2003) varen permetre reduir aquest elevat nombre d'oospècies, deixant com a valides només 17 de les 24 ooespècies inicials.

Si ens centrem a la zona del Prepirineu, han estat descrites fins a sis ooespècies de *Megaloolithus* (Vianey-Liaud i López-Martínez, 1997; Escuer *et al.*, 2003, 2006; Bravo *et al.*, 2005; Vila *et al.*, 2011), tot i la qüestionable validesa d'alguna d'elles. A més a més, tots aquest ootaxons es concentren en un període de temps relativament curt (aproximadament uns 6,5 ma.), la qual cosa no coincideix amb la diversitat faunística de sauròpodes, observada a partir de restes d'ossos (Vila *et al*., 2012), per el mateix interval de temps (Panadès i Blas, 2002).

A un nivell més general, la diversitat oològica de dinosaures reconeguda fins ara no es correspon a la diversitat faunística obtinguda a partir del registre osteològic i icnològic; ja que, dels quatre grups de dinosaures presents en base a ossos o petjades (hadrosaures, nodosaures, sauròpodes i teròpodes) només dos d'ells han estat reconeguts en base a les seves restes d'ous i closques fòssils.

Finalment, s'ha constatat que les ooespècies de *Megaloolithus* poden tenir un valor com a marcadors biocronològics en dipòsits continentals del Cretaci superior (Vianey-Liaud et al., 1994; Garcia i Vianey-Liaud, 2001b; Vila *et al*., 2011, entre d'altres). Tan mateix, entre els afloraments de banda i banda del Prepirineu s'hi han observat lleugeres diferencies pel que fa a les associacions oològiques.

Així doncs, i vista la riquesa, diversitat i potencial del registre d'ous de dinosaure del Prepirineu català, es varen plantejar un seguit d'objectius com a base dels treballs per una tesi doctoral. En primer lloc es feia necessari dur a terme una revisió sobre la validesa de les diverses ooespècies incloses al gènere *Megaloolithus*, així com la revisió dels caràcters diagnòstics emprats per les classificacions parataxonòmiques per aquest grup i, eventualment, proporcionar-ne de nous. També es va plantejar avaluar el grau de completesa del registre oològic (fins a quin punt el nombre d'espècies descrites és reflex del registre faunístic de dinosaures del Cretaci terminal), o en tot cas esclarir les causes d'un possible biaix en la diversitat parataxonòmica. En aquest punt, els estudis estratigràfics i sedimentològics duts a terme en els jaciments amb ous de dinosaure han d'aportar noves dades per conèixer quins serien els factors causants d'aquest possible biaix: de mostreig, tafonòmics, paleoambientals o faunístics. Finalment, també es planteja dur a terme estudis biostratigràfics locals basats en les associacions oològiques de *Megaloolithus* al Sinclinal de Coll de Nargó i les Conques d'Àger i Tremp, comparant els resultats amb els obtinguts per altres autors en les conques catalanes i franceses. Finalment, en el cas que les hipòtesis proposades tinguin prou consistència, es preveu proposar una biostratigrafia basada en *Megaloolithus* per a tot el Sud d'Europa.

ESTRUCTURA DE LA TESI

El present projecte de tesi es divideix en quatre grans blocs centrat en l'estudi dels següents temes:

1. Contextualitzar l'àrea d'estudi i la problemàtica oològica
2. Descriure i classificar noves restes fòssils i revisar la sistemàtica establerta
3. Avaluar la diversitat de dinosaures i altres rèptils en base a les restes d'ous
4. Proposar el registre oològic com a complement biostratigràfic.

1. INTRODUCCIÓ, GEOLOGIA I METODOLOGIA

Els primers apartats de la tesi (**capítols 1, 2 i 3**) es centren en contextualitzar a nivell històric, espacial i temporal el registre oològic del Cretaci superior de Catalunya, així com la metodologia emprada en l'estudi d'aquestes restes. En el primer capítol de la tesi (**capítol 1**) es realitza una revisió històrica de la recerca paleontològica lligada a les restes d'ous fòssil a les conques cretàciques catalanes. Es posa de manifest que aquest registre està representat per postes senceres i parcials, ous i closques de dinosaures. Aquests fòssils es troben en quatre comarques: La Noguera, el Pallars Jussà, l'Alt Urgell i el Berguedà. En destaca l'hegemonia de restes associades a *Megaloolithus*, les quals representen aproximadament el 90% del registre oològic dinosaurià conegut a Catalunya. Fins el moment s'havien realitzat estudis enfocats a l'estudi sistemàtic de les restes fòssil (Vianey-Liaud i López-Martínez, 1997; Peitz, 2000 a, b; Escuer *et al.*, 2006; Vila *et al.*, 2011), així com la seva distribució biostratigràfica (Vianey-Liaud i López-Martínez, 1997; Bravo *et al.*, 2005; Vila *et al.*, 2011) i les implicacions lligades a factors reproductius i de comportament de nidificació dels dinosaures (Jackson *et al.*, 2008; Vila *et al.*, 2010 a, b, c). Els resultats d'aquests treballs han estat reconeguts a nivell mundial, denotant la importància del registre oològic de dinosaures del Cretaci superior del la zona sud-Pirinenca catalana.

La contextualització geogràfica i geològica (**capítol 2**) de les restes estudiades revela que el registre d'ous fòssils del Cretaci superior es concentra en una estreta franja geogràfica que comprèn des del Sinclinal de Vallcebre (Berguedà, provincia de Barcelona), en la seva part més oriental, fins a límit més occidental del territori català, a la comarca del Pallars Jussà (provincia de Lleida). Això implica que el registre oològic català es localitza principalment en quatre àrees: el Sinclinal de Vallcebre, el Sinclinal de Coll de Nargó i la les conques d'Àger i Tremp. S'han descobert nombrosos jaciments amb restes d'ous i closques de dinosaures, situats tots ells en les parts baixes de la Formació Tremp (Unitat Grisa i Unitat Vermella Inferior) i més rarament de la zona més alta de la Formació Gresosos de Arèn. Tot i que possiblement l'origen sedimentari de les conques sedimentaries estudiades sigui el mateix, la potència i l'edat dels materials dipositats presenta variacions, de forma que les formacions descrites presenten certa heterocronia. Tot i això, es pot considerar que les restes d'ous de dinosaure del Prepirineu es troben en un interval temporal comprès entre el Campanià superior fins al Maastrichtià terminal (Riera *et al.*, 2009).

Referent a la metodologia d'estudi de les restes d'ous i closques fòssils (**capítol 3**) emprada en la present tesi, es poden diferenciar dos sub-apartats. En el primer d'ells (**capítol 3.1**), es descriuen les diverses metodologies utilitzades per a l'anàlisi de les mostres a estudiar, així com els processos d'obtenció i preparació de les mostres. En aquest apartat se'n destaca l'ús de nous productes i procediments de preparació per a les closques carbonàtiques fòssils (Val *et al.*, 2010) d'on se'n extreu que els millors mètodes per preparar-les és l'ús de KOH (hidròxid potàssic) i EDTA 5%. En el segon sub-apartat (**capítol 3.2**), es fa una introducció als conceptes generals de parataxonomia i classificació parataxonòmica d'ous amniotes. Es descriu la terminologia utilitzada per a la descripció d'aquestes restes fòssil, així com els diferents morfotipus estructurals de closca que es poden identificar dins els ous amniotes.

2. SISTEMÀTICA I FILOGÈNIA

En els següents capítols es recopila tota la informació disponible sobre el registre oològic de dinosaures i es descriuen en detall les restes recuperades al Cretaci superior del Prepirineu, fent noves aportacions a la sistemàtica (**capítols 4 i 5**) i establint una proposta de filogènia basada en els caràcters estructurals de les closques d'ou (**capítol 6**). Degut a la gran quantitat i diversitat d'aquestes restes, s'ha diferenciat entre ous associats a sauròpodes (**capítol 4**) i restes vinculades a altres taxons de dinosaures (**capítol 5**).

En la primera part del capítol 4 (**sub-apartat 4.1**) es du a terme una revisió completa del registre fòssil d'ous i closques atribuïdes a dinosaures sauropodomorfes. Es posa de manifest que aquest registre s'estén durant un important lapse de temps, des del Norià (Triàsic) (Bonaparte i Vince, 1979) fins el Maastrichtià final (ex. Garcia i Vianey-Liaud, 2001b; Vianey-Liaud *et al.*, 2003), i que es troben restes d'ous de dinosaure a la majoria dels continents, a excepció d'Oceania i l'Antàrtica (Mikhailov, 1997; Carpenter, 1999).

Les restes d'ous més antigues atribuïdes a sauropodomorfes daten del Triàsic superior d'Argentina (Bonaparte i Vince, 1979; Pol i Powell, 2007) i del Juràssic inferior de Sud-Àfrica (Kitching, 1979; Reisz *et al.*, 2005; 2012). En ambdós casos aquestes restes han estat associades a prosauròpodes (Reisz *et a*l., 2010). Del Juràssic es coneixen restes a França (Garcia *et al.*, 2006), Portugal (Dantas *et al.*, 1992) i a Nord Amèrica (Bray i Hirsch, 1998) i a partir d'aquest moment totes les restes descrites estan associades a grups de sauròpodes. El període Cretaci es caracteritza per ser el més ric en restes oològiques atribuïdes a sauropodomorfes. Però si ens centrem en la família Megaloolithidae, restes de *Megaloolithus* ja són presents en el Cretaci inferior on s'han trobat closques d'ous a Anglaterra (Ensom, 1997), Espanya (Kohring, 1990a; Amo-Sanjuan, 1998; Moreno-Azanza *et al.*, 2008), Tanzània (Switon, 1950; Gottfried *et al.*, 2004), Mongòlia (Grellet-Tinner *et al.*, 2011) i Argentina (Argañara, per com. 2011). D'altra banda, les restes oològiques del Cretàci superior són presents a Xina (Sochava, 1969; 1972), Mongòlia (Mikhailov, 1997), Índia (Vianey-Liaud *et al.*, 2003), Espanya (Moratalla, 1993; Vianey-Liaud i López-Martínez, 1997; Vila et al., 2011), França (Vianey-Liaud *et al*, 1994; Garcia, 2000; Garcia i Vianey-Liaud, 2001), Romania (Grigorescu e*t al.*, 1990; Grigorescu i Ciski, 2008) i Marroc (Vianey-Liaud i Garcia, 2003; Garcia *et al.*, 2003); essent representades tant per *Megaloolithus* com per *Faveoloolithus*.

Gràcies a aquesta revisió, s'han pogut establir certs paral·lelismes entre el registre d'ous i alguns dels majors esdeveniments de la història paleobiogeogràfica dels sauròpodes, suggerint que el registre fòssil d'ous pot aportar informació sobre els processo evolutius i migratoris dels dinosaures.

En el **sub-apartat 4.2**, es realitza una revisió crítica del criteris estructurals utilitzats clàssicament per a la diagnosi de la oofamília Megaloolithidae i la validesa i/o sinonímia de les ooespècies assignades a aquest grup. En una primera instància, es constata que paràmetres estructurals com són les dimensions de l'ou, el gruix de closca o el patró de porositat no poden ser considerats com a elements diagnòstics per si mateixos; mentre que el patró ornamental, el sistema de canals, la forma i el grau de fusió de les unitats de closca i la mida i densitat de les mamil·les si que són bons elements diagnòstics per els taxons de *Megaloolithus*.

A més a més, aquesta revisió ha permès identificar tres patrons estructurals bàsics dins de Megaloolithidae, referits aquí com grups MG, dins dels quals s'hi inclouen diverses ooespècies. Dins del grup MG1 s'han inclòs tres ootaxons (*Megaloolithus mamillare, M. jabalpurensis* i *M. dhorindungriensis*), dels quals dues oospècies són considerades vàlides, *M. mamillare i M. jabalpurensis*, mentre que *M. dhorindungriensis* ha estat considerat sinònim de *M. jabalpurensis*. El grup MG2 inclou inicialment cinc ooespècies (*M. aureliensis, M. petralta, M. baghensis, Pseudomegaloolithus atlasi* i *Patagoolithus salitralensis*), de les quals només 2 són considerades vàlides (*M. aureliensis* i *M. baghensis*). El grup MG3 inclou set ootaxons: *M. cylindricus, M. khempuriensis, M. megadermus, M. microtuberculata, M. mohabeyi, M. padiyaliensis* i *M. siruguei*. En aquest grup, *M. megadermus* es considera un *nomen dubium* ja que podra correspondre a closques patològiques, *M. microtuberculata* és considerat un sinònim de *M. siruguei*, de la mateixa manera que *M. padiyaliensis* ho és de *M. mohabeyi*. Així doncs, només quatre ooespècies es mantenen vàlides dins d'aquest grup (*M. cylindricus, M. khempuriensis, M. mohabeyi* i *M. siruguei*).

Finalment, *M. maghrebiensis*, que no ha estat classificat en cap dels grups anterior, per la seva combinació única de caràcters, es considera un ootaxó vàlid, mentre que *M. problematica* és re-assigna a *Spheroolithus problematica* nov. com. Per tant, de les 17 ooespècies considerades vàlides prèvies a la revisió, només 10 es mantenen com a vàlides.

Finalment, en el **sub-apartat 4.3** es descriuen en detall les ooespècies de *Megaloolithus* presents en el Cretaci superior del Pirineu sud-central, tenint en compte les consideracions taxonòmiques i la validesa de les ooespècies esmentades anteriorment. Així doncs, s'han identificat quatre ooespècies de *Megaloolithus*: *M. aureliensis*, *M. siruguei*, *M. mamillare* i *M. baghensis*. De totes elles *M. siruguei* és l'ootaxó més ben representat, essent present en totes les conques fini-cretàciques del Prepirineu, mentre que *M. aureliensis* ésel menys freqüent, essent representat únicament en quatre jaciments de les Conques d'Àger i Tremp (Moratalla, 1993; Vianey-Liaud i López-Martínez, 1997) i en el Sinclinal de Coll de Nargó. La ooespècie *M. mamillare* ha estat reconeguda tant a les Conques de Àger i de Tremp com a al Sinclinal de Vallcebre (Vila et al., 2011), però no al Sinclinal de Nargó; mentre que *M. baghensis* és present a totes tres conques.

Referent als ootaxons no afins a sauròpodes (**capítol 5**) s'ha volgut diferenciar, d'una banda, l'oogènere *Cairanoolithus* (**sub-apartat 5.1**) i ,per l'altra, tota la resta de material oològic que serveix per completar el registre oològic del Prepireneu (**sub-apartat 5.2**). Aquesta diferenciació es basa en el fet que *Cairanoolithus* ha estat llargament considerat el grup germà de *Megaloolithus* (Vianey-Liaud et al., 1994). Tan mateix, la descoberta de nou material assignat a aquest ootaxó en el Sinclinal de Coll de Nargó ha proporcionat nova informació.

Així doncs, en el **sub-apartat 5.1**, es descriu per primera vegada la presència de l'oogènere *Cairanoolithus* al Sud dels Pirineus. Aquest material representa la primera evidència d'aquest ootaxó fora de França, el qual havia estat considerat un oogènere endèmic d'aquesta regió. Les diferències estructurals significatives observades entre *Cairanoolithus* i *Megaloolithus* qüestionen la afinitat entre ambdós tipus d'ous, posant de manifest la creació d'una nova classificació per el material atribuït a *Cairanoolithus*. D'aquesta manera es proposa erigir una nova oofamília (Cairanoolithidae nov. oofam.) que inclou les restes trobades a Coll de Nargó, les dues ooespècies formalment descrites a França (Vianey-Liaud *et al.*, 1994; Garcia i Vianey-Liaud, 2001a) i el material de Bouches-du-Rôhne (Cousin, 2002). A més a més, es posa de manifest l'afinitat microestructura entre aquest nou grup parataxonòmic amb les oofamílies Spheroolithidae i Ovaloolithidae, ambdues relacionades amb dinosaures ornitòpodes (Horner i Makela, 1979; Horner i Curry, 1994; Mikhailov, 1997).

D'altre banda, en el **sub-apartat 5.2**, es descriuen les primeres restes europees del oogènere *Spheroolithus*, les quals, en base a la seva configuració microestructural, poden ser considerades com a nou ootaxó afí als ous de *Maiasaura* d'Amèrica del Nord (Horner i Makela, 1979; Horner i Curry, 1994). En aquest mateix capítol, es descriuen noves ooespècies assignades al oogènere *Prismatoolithus*, el qual es troba representat com a mínim per sis ootaxons. Dos dels ootaxons són presents al sud de França (*P. matellensis* i *P. tenuis;* Vianey-Liaud i Crochet, 1993), un altre es afí a *P. levis* de Nord Amèrica (Zelenitsky i Hills, 1996) i dos altres representen nous ootaxons mai descrits. D'altra banda, destaquen la gran quantitat de restes assignades a *Pseudogeckoolithus*. Aquest ootaxó va ser inicialment assignat al oogènere *Prismatoolithus* (Vianey-Liaud i López-Martínez, 1997), però el nou material estudiat proporciona noves dades i informació,que suggereixen una major afinitat amb els ous dels llangardaixos actuals. Finalment, s'ha descrit la presència de *Ageroolithus*. Aquest ootaxó es troba escassament representa i podria estar relacionat bé amb dinosaures teròpodes bé amb ocells tipus ratite.

La filogènia i les implicacions taxonòmiques dels oogèneres *Megaloolithus* i *Cairanoolithus* són tractats en el **capítol 6**. Els resultats obtinguts a partir de les anàlisis filogenètiques realitzades en les ooespècies assignades a *Megaloolithus* (**sub-apartat 6.1**), mostren que aquestes es poden classificar en tres grups estructurals ben diferenciats, tal i com s'havia apuntat anteriorment en el **sub-apartat 4.2**. A més, algun d'aquests taxons mostra una gran similitud amb el gènere *Spheroolithus*. Això s'ha interpretat com a possible convergència evolutiva relacionada amb factors ambientals limitants o a la fisiologia reproductiva dels organismes ponedors. També podria ser que tant els ous dels sauròpodes com els de hadrosaures retinguessin caràcters ancestrals típics dels ous d'arcosaures. Finalment, els resultats obtinguts també apunten a que *Faveoloolithus*, un ootaxó clàssicament associat de forma indirecta a sauròpodes, podria tractar-se, de fet, d'una ooespècie de *Megaloolithus* altament derivada.Tal i com s'ha mencionat en apartats anteriors (**sub-apartat 5.1**), *Cairanoolithus* ha estat llargament considerat com a taxó germà de *Megaloolithus*, tot i que caràcters estructurals observables contradiuen aquesta interpretació. Els resultats dels anàlisis filogenètics duts a terme (**sub-apartat 6.2**) agrupen *Cairanoolithus* conjuntament amb *Spheroolithus* i *Ovaloolithus.* Alhora, aquests tres oogèneres constituirien un grup clarament diferenciat a *Megaloolithus*. Tot i l'absència de material fòssil de que confirmi les nostres suposicions, basant-se en les afinitats taxonòmiques es pot concloure que *Cairanoolithus* podria haver estat produït per dinosaures ornitòpodes.

3. OODIVERSITAT I REGÍSTRE FÒSSIL

En el tercer gran apartat de la present tesis (**capítol 7**), es realitza l'estudi referent a la diversitat oològica del Prepirineu català, les seves variacions al llarg del Campanià i Maastrichtià i la seva possible relació amb les faunes de dinosaures d'aquest període.

En total, s'han identificat 13 ooespècies diferents pel Cretaci superior dels Pirineus sud-centrals. Aquesta diversitat és només equiparable a la descrita en territori francès (Garcia, 2000), mentre que la diversitat oològica és molt menor en altres jaciments del món (ex. Garcia i Vianey-Liaud, 2003; Welsh i Sankey, 2007; Jackson i Varricchio, 2010; Tanaka *et al*., 2011) . També es constata que la diversitat d'ootaxons no és constant al llarg del temps, essent major durant el Campanià superior que durant el Maastrichtià. La brusca davallada de la oodiversitat prop del límit Campanià-Maastrichtià podria estar relacionada amb canvis ambientals sobtats. D'altra banda, la variació de la oodiversitat al llarg de temps podria reflectir preferència de zones de nidificació per a cada grup parataxonòmic, ja que no s'ha pogut establir una relació directe entre l'absència/presència de cada ootaxó i la dels seus organismes ponedors. D'aquesta manera, tant els ous de teròpodes (*Prismatoolithus*) com els ous assignats a ornitòpodes (*Cairanoolithus* i *Spheroolithus*) estarien concentrats en ambients costaners o pròxims a masses d'aigua més o menys permanents, mentre que els ous de sauròpode es restringirien a ambient de tipus fluvial.

Un dels principals problemes que presentava el registre d'ous de dinosaure al Prepirineu era la discordança que existia entre el nombre d'ooespècies i de taxons de sauròpodes, per el mateix interval de temps (Panadès i Blas, 2002). Malgrat l'absència de restes embriològiques en els jaciments del Cretaci superior de Catalunya que permetin assignar una categoria taxonòmica a les restes d'ous de *Megaloolithus*, en el **capítol 7** també es realitza una aproximació entre el registre oològic i osteològic associat a dinosaures sauròpodes. Aquesta aproximació té en compte la co-ocurrència temporal i espacial dels dos registres al llarg del Campanià superior i el Maastrichtià al sud d'Europa. D'aquesta manera, es demostra la coherència existent entre la diversitat de ootaxons de *Megaloolithus* i la fauna de sauròpodes coneguda per aquest interval de temps (Vila *et al*., 2012), on cada ooespècie de *Megaloolithus* pot ser atribuïda a un grup determinat de sauròpodes. D'una banda, es proposa d'associar *Megaloolithus aureliensis* a titanosaures basals com *Atzinganosaurus* de França, mentre que *Megaloolithus siruguei* podria ser relacionat amb sauròpodes litostròtids (ex. *Lirainosaurus, Ampelosaurs, Magyarosaurs*). D'altra banda, *Megaloolithus mamillare* podria pertànyer a titanosaures derivats, com els saltasaurins, en base a les descobertes embriològiques fetes a Argentina (Chiappe *et al*., 1998). La assignació taxonòmica de *Megaloolithus baghensis* és força més complicada d'avaluar. Tenint en conte el registre de sauròpodes de Sud Amèrica i la seva co-ocurrència amb *M. baghensis*, se'n deriva que aquest ootaxò podria estar relacionat amb aeolosaurids. Tan mateix, aquest grup de sauròpodes no ha estat reconegut fins ara a Europa (Vila *et al*., 2012).

4. BIOSTRATIGRAFIA

El quart i últim apartat de la present tesi (**capítol 8**) s'ha centrat en l'estudi biostratigràfic de les restes oològiques assignades a *Megaloolithus*. S'han proporcionat noves dades i informació sobre les successions oològiques en les conques de Coll de Nargó, Àger i Tremp, juntament amb la revisió i actualització de la biostratigrafia de *Megaloolithus* a Europa.

És àmpliament acceptat que les ooespècies del tipus *Megaloolithus* poden ser utilitzades com a marcadors biocronològics (Garcia i Vianey-Liaud, 2001b; Bravo *et al*., 2005; Vila *et al*. 2011). Aquest elements són realment útils per datar sediments continentals del Cretaci superior que sovint són escassos en restes fòssils amb potencial cronostratigràfic (ex. algues caròfites). És per aquest motiu que un estudi detallat de les restes oològiques pot aportar informació valuosa per a la datació dels jaciments de finals del Cretaci.

En primer lloc, cal destacar que durant molt de temps s'ha fet un us incorrecte de la terminologia emprada en aquesta tipologia d'estudis biostratigràfics. Per aquest motiu, el terme "assemblage" (conjunt) és reemplaçat pel de "oozone" (oozona), ja que aquesta terminologia és més acurada que la prèviament mencionada.

Referent a la biostratigrafia de les conques cretàciques catalanes el Prepirineu s'han obtingut els següents resultats:

Al Sinclinal de Coll de Nargó s'han identificat tres oozones diferents. La oozona més basal està formada per l'associació dels ootaxons *M. aureliensis*, *M. siruguei* i *Cairanoolithus*, coincidint amb la part alta del "Assemblage 1" descrit a França (Garcia i Vianey-Liaud, 2001b). La següent oozona es caracteritza per estar constituïda exclusivament per *M. siruguei* i equivaldria al "Assemblage 2" (*sensu* Vila et al., 2011). La última oozona que es troba al Sinclinal de Coll de Nargó està format per la única presència del ootaxó *M. baghensis* i correspondria parcialment al "Assemblage 3" de Garcia i Vianey-Liaud (2001b). Les associacions oològiques i la seva successió estratigràfica ha permès establir que els jaciments fossilífers del Sinclinal de Coll de Nargó estan compresos entre el Campanià terminal i la part baixa del Maastrichtià superior.

La mateixa metodologia d'estudi ha estat aplicada en les conques d'Àger i Tremp, amb els següents resultats: s'ha identificat tres oozones similars a les descrites prèviament a Coll de Nargó. La oozona inferior està composta per la presencia de *M. aureliensis* i *M. siruguei,* equivalent al "Assemblage 1" (*sensu* Garcia i Vianey-Liaud, 2001b). La següent oozona està formada únicament per la presència de *M. siruguei*, essent només identificada en dos jaciments. La oozona superior està formada per la co-ocurrència de les ooespècies *M. mamillare* i *M. baghensis*, essent correlacionable amb "Assemblage 3" de Garcia i Vianey-Liaud, 2001b.

A mode de revisió prèvia a la proposta d'una biostratigrafia general a nivell europeu, s'han revisat els materials provinent de altres conques fini-cretàciques del sud dels Pirineus. D'una banda, el material oològic provinent del Sinclinal de Vallcebre ha estat estudiat per Vila *et al*. (2011). En aquest treball es descriu la presencia d'una espècie indeterminada de *Megaloolithus* (*Megaloolithus* sp.). La revisió d'aquest material ha permès reassignar-lo a la ooespècie *M. baghensis*, fent que l'última associació oològica d'aquesta conca sigui igual a la última oozona descrita prèviament per les conques d'Àger, Tremp i Coll de Nargó. López-Martínez *et al*. (1999) van descriure la possible presència d'una ooespècie de *Megaloolithus* afí a *M. pseudomamillare* (= *M. baghensis sensu* Vianey-Liaud *et al*., 2003) al jaciment de Blasi-2, a Aragó. La revisió d'aquest material ha demostrat que les restes han estat erròniament interpretades, ja que les característiques estructurals que presenta el material oològic és clarament atribuïble al tipus crocodilià.

Així doncs, aquest estudis previs han permès la revisió i actualització de la bioestratigrafia basada en la successió d'ooespècies de *Megaloolithus* a Europa, permetent descriure tres oozones, les quals poden ser reconegudes al Nord-Est de la Península Ibèrica, al Sud de França i a Romania:

1) Oozona de *M. aureliensis* + *Cairanoolithus*: Està formada per la possible coexistència de *M. aureliensis, M. siruguei* i l'òogènere *Cairanoolithus*. Malgrat que no es coneix la posició exacte de la base d'aquesta oozona, s'estén més enllà del cron C33n. D'altra banda, el sostre d'aquesta oozona es situa a prop del límit entre els crons C32n.1n i C31r (Campanià superior). Aquest límit està marcat per la última presència de *M. aureliensis* i *Cairanoolithus.*

2) Oozona de *M. siruguei*: Està caracteritzada per presència única de l'ooespècie *M. siruguei*. El límit superior d'aquesta oozona es troba situat a prop del canvi de polaritat magnètica entre els crons C31r i C31n (Maastrichtià superior), el qual es caracteritza per la última presència de *M. siruguei* i la primera aparició de *M. mamillare.*

3) Oozona de *M. mamillare* + *M. baghensis*: Es defineix per la possible co-ocurrència de les ooespècies *M. mamillare* i *M. baghensis*. La primera presència de *M. mamillare* es situa prop del límit C31r-C31n, mentre que la primera aparició de *M. baghensis* es una mica més moderna. El límit superior d'aquesta oozona està marcat per la última aparició de *M. baghensis,* prop de la base del cron C29r.

Això comporta que les restes més modernes d'ous de dinosaures es situïn aproximadament uns 200.000 anys abans del límit Cretaci/Paleogen.

CONCLUSIONS

El present projecte de tesi ha proporcionat noves dades i informació en base al registre fòssil d'ous de dinosaures del Prepirineu. Les principals conclusions que s'extreuen d'aquest estudi són:

- El registre d'ous atribuïts a dinosaures sauropodomorfes s'estén des del Norià fins els Maastrichtià superior, essent present a la majoria de continents. La distribució paleogeografia i temporal d'aquest registre pot ser relacionat amb alguns dels esdeveniments més importants d'aquest grup de dinosaures.
- S'ha qüestionat la validesa d'alguns caràcters estructurals utilitzats clàssicament per a la descripció de *Megaloolithius*, alhora que se'n ha aportat de nous.
- La mida del ou, el gruix de closca o la morfologia de les obertures dels porus de respiració no es poden considerar en si mateixos caràcters diagnòstics, ja que sovint estan lligats a factors de variació interespecífica.
- La forma de les unitats, el seu grau de fusió, l'ornamentació i el sistema de canals de respiració es

consideren caràcters vàlids per a la identificació de les ooespècies *de Megaloolithus*.

- La mida i densitat de mamil·les de la part interna de les closques dels Megaloolithus se proposa com a possible nou caràcter diagnòstic, doncs aquest caràcter està estretament lligat a processo biològics de desenvolupament embrionari i ,per tant, té implicacions taxonòmiques.

- S'ha pogut establir tres grups estructurals bàsics que permeten classificar les ooespècies de la oofamília Megaloolithuidae, cada un amb les seves pròpies característiques estructurals.

- Dels 20 ootaxons atribuïts inicialment a la oofamília Megaloolithidae, només 10 són considerats vàlid després de la seva revisió. Destaca la reevaluació de *M. megadremus* com a *nomen dubium* i *Spheroolithus problematica* nov. com., ambdos provinents del subcontinent indi.

- S'ha constatat la presència de quatre ootaxons de *Megaloolithus* al Cretaci superior de Catalunya (*M. aureliensis, M. siruguei, M. mamillare* i *M. baghensis*).

- L'estudi de les primeres restes de *Cairanoolithus* trobades al sud dels Pirineus posa de manifest la necessitat de crear una nova oofamília (Cairanoolithidae nov. oofam.). A més, aquestes restes han estat atribuïdes taxonòmicament a dinosaures ornitòpodes.

- Els estudis filogenètics posen de manifet les observacions realitzades anteriorment com la presència de tres grups estructurals dins de *Megaloolithus*. A més, es proposa una nova relació entre *Megaloolithus* i *Faveoloolithus*, on aquest últim ootaxó correspondria a un megaloolithid molt derivat.

- Les similituds estructurals entre ous de sauròpode (*Megaloolithus*) i ornitòpode (*Cairanoolithus* i *Spheroolithus*) poden ser degudes a un cas d'homoplàsia i/o retenció de caràcters ancestrals.

- Es conclou que el registre oològic del Cretaci superior de Prepirineu consta de 13 ootaxons, entre els quals destaquen les primeres restes oològiques de hadrosaure (*Spheroolithus*) d'Europa i nous ootaxons de *Prismatoolithus*.

-Es posa de manifest que l'oogènere *Pseudogeckoolithus*, relacionat tradicionalment amb dinosaures teròpodes, presenta prou caràcters microestructurals com per associar-lo a llangardaixos.

- La diversitat oològica del Prepirineu, a nivell mundial, és únicament equiparable a la descrita al sud-est de França.

- Aquesta diversitat oològica es distribueix de forma no uniforme al llarg del Campanià-Maastrichtià, on la major diversitat es concentra a les parts baixes dels dipòsits continentals. També es destaca la brusca reducció de la diversitat a principis del Maastrichtià inferior, que es recupera lleugerament a partir del Maastrichtià superior.

- Aquestes diferències en el registre s'han relacionat amb dos possibles factors:

  1) La brusca davallada de la oodiversitat a principis del Maastrichtià podria estar relacionada amb canvis climàtics que van tenir lloc durant el Campanià superior i el Maastrichtià inferior. La relativa estabilitat climàtica del Maastrichtià superior hauria afavorit la recuperació de les "oofaunes".

  2) El registre oològic podria estar condicionat a factors de comportament reproductiu, és a dir, que cada ootaxó estaria associat a un ambient sedimentari determinat i aquest patró quedaria enregistrat en el registre fòssil.

- S'ha intentat vincular cada una de les ooespècies de *Megaloolithus* amb l'actual fauna de sauròpodes coneguda al sud d'Europa. Com a resultat d'aquesta aproximació, s'ha conclòs que: *M. aureliensis* podria ser vinculat a titanosaures basals; *M. siruguei* a sauròpodes litostròtids; *M. mamillare* a titanosaures derivats (ex. Saltasaurins); *M. baghensis* pot ser vinculat a aeolosàurids (grup no present a Europa).

- Referent a les implicacions biostratigràfiques de les closques d'ou de *Megaloolithus*, s'han realitzat dos estudis detallats a nivell de conca (Coll de Nargó i conques d'Àger i Tremp) i una actualització de la biostratigrafia general a nivell europeu.

- Es proposa instaurar una nova terminologia per caracteritzar els intervals amb ous. El terme "oozona" substitueix el terme "assemblage" proposat per Garcia i Vianey-Liaud (2001b).

- L'estudi biostratigràfic al Sinclinal de Coll de Nargó a obtingut els següents resultats:

  1) Presència de tres ooespècies de *Megaloolithus* (*M. aureliensis, M. siruguei*, *M. baghensis*) i de *Cairanoolithus* distribuïdes al llarg de la secció estrairgàfica.

  2) Identificació de tres oozones: Oozona *M. aureliensis* + *Cairanoolithus*; Oozona *M. siruguei*; Oozona *M. mamillare* + *M. baghensis*.

  3) Aquestes associacions han permès delimitar l'edat els jaciments amb ous de dinosaure del Sinclinal de Coll de Nargó, els quals s'estenen des del Campanià superior fins a inicis del Maastrichtià superior.

- L'estudi biostratigràfic de les conques de Tremp i Àger ha obtingut els següents resultats:

  1) Presència de quatre ooespècies de *Megaloolithus* (*M.aureliensis, M. siruguei*, *M. mamillare*, *M. baghensis*) distribuïdes al llarg de la secció estrairgàfica.

  2) Identificació de tres oozones: Oozona *M. aureliensis* + *Cairanoolithus*; Oozona *M. siruguei*; Oozona *M. mamillare* + *M. baghensis*.

  3) Aquestes associacions han permès delimitar l'edat els jaciments amb ous de dinosaure de les conques de Tremp i Àger, els quals s'estenen des del Campanià superior fins finals del Maastrichtià superior.

- La revisió del material oològic provinent del Sinclinal de Vallcebre a confirmat la presencia de *M. baghensis* en aquesta area, ratificant la presencia de la oozona Oozona *M. mamillare* + *M. baghensis* en aquest sector.

- Una visió més àmplia de les successions oològiques de *Megaloolithus* ha permès actualitzar l'actual coneixement d'aquesta temàtica a nivell Europeu, refinant la situació de cada oozona:

  1) Oozona *M. aureliensis* + *Cairanoolithus*: Caracteritzada per la possible co-ocurrència de *M. aureliensis, M. siruguei* i *Cairanoolithus*. La base de la oozona no està ben delimitada però es situa dins del cron C33 (Campanià mig). El sostre de la oozona el marca l'última presència de *M. aureliensis* i *Cairanoolithus* en el registre fòssil, esdeveniment que té lloc prop del canvi de cron C32n.1n i C31r (finals del Campanià superior).

  2) Oozona *M. siruguei*: Caracteritzada per la única i possible presència de *M. siruguei.* La base de la oozona coincideix amb el sostre de la oozona *M. aureliensis* + *Cairanoolithus* (prop del canvi entre C32n.1n i C31r, finals del Campanià superior). El sostre de la oozona ve marcat pel reemplaçament de la ooespècie *M. siruguei* per *M. mamillare*, que té lloc prop del límit entre els crons C31r i C31n (inicis del Maastricthià superior).

3) Oozona *M. mamillare* + *M. baghensis*: Caracteritzada per la possible co-ocurrència de *M. mamillare* i *M. baghensis*. La base de la oozona coincideix amb el sostre de la oozona *M. siruguei* (prop del límit entre C31r i C31n, inicis del Maastricthià superior). El sostre de la oozona ve marcat per la última presència de *Megaloolithus* en el registre fòssil, que té lloc dins el cron C29r (finals del Maastricthià superior).

- Es destaca que la última resta atribuïda a *Megaloolithus* al sud d'Europa es situa a 0.2 Ma abans del límit Cretaci/Paleogen.

PROLOGUE

Motivation, Problematic and Objectives

MOTIVATION

Dinosaurs have fascinated humanity since the first iguanodon reconstructions created by W. Hawkins, which strongly impacted to the Victorian public in the middle nineteenth century. Since then, the paleontology of dinosaurs has grown both in a scientific and a popular way. Nevertheless, discoveries and interest on Mesozoic reptiles has not been uniform all over the world. First dinosaur discoveries in southern Pyrenean slope were made in the first quart of the twentieth century, with the discovery of some isolated bones in the Tremp Basin. Later on, in the middle fifties, European scientists followed the clues of this first discovery and began to deal with systematic prospection that showed the potentiality of this region. More than fifty years later, the research on dinosaurs and their world are a discipline strongly established in the scientific community of Catalonia. Most of this fossil record has been recorded in the Arén Sandstone and Tremp Formations of different basins in South-Central Pyrenees, providing new data with each new discovery.

In the Pyrenees, paleontological science not focused only with classic studies on dinosaur systematic but also with a great purpose: the reconstruction and comprehension of Late Cretaceous ecosystems. Focused in this goal, paleontologists and geologists from Institut Català de Paleontologia Miquel Crusafont (ICP), Universitat Autònoma de Barcelona (UAB) and Universitat de Barcelona (UB) have worked together during the lasts years for building a rigorous scenario of fauna, flora and geological background of Pre-Pyrenees of more than 65 million years ago.

As part of this purpose, the present thesis provides new data and information about a fossil record sometimes left. Most of Mesozoic vertebrate fauna were oviparous, which implies that they laid eggs. Dinosaurs, as reptiles, were also oviparous and remains of their eggs have conserved fossilized until today. This fossil record, known as oological record, is still not well understood in Southern Pyrenees even its study should provide key data to deepen into diversity, paleobiology and systematic of the last European dinosaurs.

PROBLEMATIC

Despite the high diversity of fossil eggs in southern Pyrenees (Vianey-Liaud and López-Martínez, 1997; López-Martínez *et al.*, 1999; López-Martínez, 2000), *Megaloolithus*, a type of fossil egg associated to sauropod dinosaurs, is the most common fossil egg in the South Pyrenees, representing up to 90% of the whole oological record known for this area. In fact, megaloolithid eggs are one of most abundant Cretaceous dinosaur egg-type in the world. Due to that condition, there is great number of paleontological studies focused in their systematic classification and diversity during the end of Mesozoic era. In parataxonomical classifications published at the end of the last century, Megaloolithidae oofamily counted with three oogenus and twenty-four oospecies, all of them concentrated between the Early Campanian and the Late Maastrichtian (Carpenter, 1999). Some authors pointed out the great similarity between some oospecies of *Megaloolithus* from Indian, South American and European (Vianey-Liaud *et al.*, 1987, 1994; Calvo *et al.*, 1997, among others). This condition led Vianey-Liaud *et al.* (2003) to conclude that only seventeen of initial twenty-four oosspecies of *Megaloolithus* were valid.

In South-central Pyrenees up to six megaloolithid oospecies have been recognized (Vianey-Liaud and López-Martínez, 1997; Escuer *et al.*, 2003, 2006, Bravo *et al.*, 2005; Vila *et al.*, 2011), although some of them are dubiously valid. Even more, this diversity of *Megaloolithus* is apparently too high for a relatively short time span (approx. 6.5 My); and it does not match with current known sauropod diversity for the same interval of time (Panadès i Blas, 2002). Thus, it seems necessary to reevaluate the validity of current megaloolithuid oospecies, with special attention to European ones. A review of diagnostic structural characters should be required for this group of fossil eggs and, if necessary, new criteria of classification should be proposed. This problem involves *Megaloolithus*, with its high oological diversity versus the known sauropod diversity.

On the other hand, in Southern Pyrenees, dinosaurs are represented by four different groups, mainly identified by bones. Ornithopods are the most common group of dinosaurs in this area, being represented for euhadosaurs, different types of hadrosaurs, and lambeosaurs (e.g. *Pararhabdodon, Arenysaurus or Blasisaurus)*; while nodosaurian ankylosaurs is the less known in this fossil record, only being identified by very scarce elements. Sauropods are known by scarce osteological elements, but their presence is also indirectly interpreted based on ichnofossils remains (i.e. footprints and eggs). Finally, theropods are mainly known by teeth elements, very scarce bone fragments and footprints (see for more details Riera *et al.*, 2009 and references herein). However, only the two last groups of dinosaurs, sauropods and theropods, have been recognized in the oological record. This situation suggests two main lines of research:

1) The first line is focused on the incompleteness of current oological record in Southern Pyrenees, which includes six ootaxa of sauropod, three of theropod and one of ornithoid (Vianey-Liaud and López-Martínez, 1997; Escuer el al, 2006), and the apparent absence of hadrosaur eggs.
2) The second line involves the relationship between oological and dinosaur taxa diversities during the end-Cretaceous in South-Central Pyrenees. Why they do not match? Could the oological record be influenced by sampling, taphonomical or paleoenvironmental factors?

Finally, it is widely accepted that oospecies of *Megaloolithus* can be used as biostratigraphical markers (Vianey-Liaud *et al.*, 1994; Vianey-Liaud and López-Martínez, 1997; Garcia and Vianey-Liaud, 2001b; Vila *et al.*, 2011) in the Late Cretaceous of Europe. According to eggs associations and their stratigraphical succession it is possible to establish three assemblages each one characterizing a specific interval of time. However, there are some differences in the *Megaloolithus*'s succession between Northern and Southern Pyrenees (Vianey-Liaud and López-Martínez, 1997; Vila *et al.*, 2011).

OBJECTIVES

The main goal of this thesis is to provide new data and information about the diversity of the oological fossil record and its implication in the Upper Cretaceous (Late Campanian- Late Maastrichtian) in the South-central Pyrenees, with special attention on megaloolithid eggs.

This main objective can be divided into five sub-objectives:

1) To establish new and useful structural criteria for the classification and identification of *Megaloolithus* oospecies.
2) To redefine the number of valid oogenus and oospecies for the oofamily Megaloolithidae, and determinate which of them are present in the Upper Cretaceous of South-central Pyrenees.
3) To determine the diversity of the oological record of South-central Pyrenees during the end-Cretaceous time and describe new taxa.
4) To evaluate if the oological diversity is consistent with dinosaur diversity for the same time interval or if this relationship is influenced by other factors (e.g. sampling, taphonomy, paleoenvironment…).
5) To build a biostratigraphy of *Megaloolithus* per each studied basin (Coll de Nargó Syncline and Àger and Tremp basins), inferring their age, and update and propose a unique European megaloolithid biostratigraphy.

SECTION 1

Introduction and Contextualization

Chapter 1

HISTORICAL OVERVIEW ON THE STUDY OF DINOSAUR EGGS: SPECIAL ATTENTION TO SOUTH-CENTRAL PYRENEES RECORD AND PROBLEMATIC

When in 1824 Richard Buckland described the first dinosaur, *Megalosaurus*, which literally means "gigantic lizard", he already pointed out the possible relationship between this group of extinct animals and extant reptiles. This implied a succession of attributes related to reproductive biology of dinosaurs. Given that most of the reptiles (excluding some lizard and snakes) have oviparous reproduction, were dinosaurs oviparous? Nowadays this is well known, but the theory of dinosaur's oviparity needed hundred years to be confirmed.

First known references of fossil eggs and eggshells appear a decade after Owen defined the term Dinosauria as a "distinct tribe or sub-order of Saurian Reptiles", which was firstly recognized in England and, later on, in the rest of the world (see Buckman, 1859; Pouech, 1859; Meyer, 1860, 1867; Carruthers, 1871). It seems clear that Dr. Phillip Matheron was the first who identified fossil eggs in Aix-en-Provence (France) (Taquet, 2001) in 1846. However, he did not publish his discoveries until after twenty-three years (Matheron, 1869). The first scientific reference about dinosaur eggs is attributed to Abbot Pouech (1859). Pouech showed the presence of big fossil bones and thick eggshell fragments from Mas d'Azil (Provence, France), and he suggested that those eggshells might be related to big reptiles or birds. Later on, Matheron (1869) established a plausible relationship between those big fragments of fossil eggs and fossil bones, which were attributed to *Hypselosaurus* (Matheron, 1868). Even so, he never ruled out the possible attribution of French oological remains to large birds (i.e. *Aepyornis*).

Gervais (1877) attempted to solve that problem performing the first thin sections of fossil eggshells and comparing them with those of modern eggs. He concluded that fossil eggshells from Provence had a similar structure as reptiles and turtles, discarding the theory of avian origin for the fossil eggshells from Provence.

Surprisingly, these studies were overlooked for the scientific community of that time, which was more interested in systematic and taxonomy of dinosaurs than in other paleobiological issues.

At the beginning of the twentieth century, the discovery of hundreds of dinosaur eggs in the Gobi Desert (Mongolia) by Roy Chapman Andrews (Andrews, 1932) aroused a great popular interest for this topic. However, it had not the same effect in the scientific community. In fact, Van Straelen (1925) was the only who performed a paleontological study about Mongolian eggs, answering the question about dinosaurs oviparity.

Nowadays, dinosaur eggs have been reported from all continents except for Australia and Antarctica. The most notable sites are located in Patagonia (Argentina), Montana (USA), Alberta (Canada), the Gobi Desert (Mongolia), some basins from China and Pyrenees (as southwestern France as northeastern Spain) (Carpenter, 1999).

Focusing in the South-central Pyrenees area, the oldest references of dinosaur eggs date from the end of the fifties. Lapparent (1958, 1959) reported the presence of big spherical eggs in Basturs site (Tremp Basin, Lleida Province). He emphasized the huge amount of fossil eggs concentrated in a relatively small area, considering that site one of the most important dinosaur egg-site in the world. Some years later, Aepler (1967) performed a geological study on the coal mines in Vallcebre (Barcelona Province), reporting the presence of big bones and dinosaur eggs. On the same year, Rosell (1967) described the occurrence of fossil eggs and eggshells near Segre River, not so far from Coll de Nargó village (Lleida Province). Those discoveries represented the beginning of a succession of paleontological works focused on the study of dinosaur eggs.

In 1979, Erben and colleges postulated a theory relating the dinosaur extinction and the increasing of pathological eggs at the end of the Cretaceous. Most of the oological material used by Erben *et al.* (1979) came from different sites of Southern Pyrenees, such as Tremp and Coll de Nargó area. So far, all those studies were made by Germanic scientists, not being until the early nineties when Spanish paleontologists showed interest for this fossil record (Moratalla, 1993; Sanz *et al.*, 1995; Vianey-Liaud and López-Martínez, 1997; Bravo and Reyes, 2000).

Although most of sites with fossil oological remain are located in the Eastern Tremp Basin, one site yielding this fossil record was discovered in the most western part of the Tremp Basin. López-Martínez (2000) reported several types of fossil eggshells from Blasi-2 site (Huesca province, North Spain), most of them attributed to ornithoid-ratite morphotype.

The quality and quantity of this oological record has allowed various types of paleontological works related with the reproductive biology of dinosaurs. These studies are mainly focused on the oological diversity (Vianey-Liaud and López-Martínez, 1997; Peitz, 2000a,b; Bravo *et al.*, 2005, Escuer *et al.*, 2006), biochronological distribution and egg assemblages (Vianey-Liaud and López-Martínez, 1997; Bravo *et al.*, 2005; Vila *et al.*, 2011) and reproductive patterns and nesting behavior of sauropod dinosaurs (López-Martínez *et al*., 2000, 2009; Fortuny *et al.,* 2007, Jackson *et al.*, 2008; Vila *et al.*, 2010a, b; Vila *et al.*, 2011).

Thanks to those works, we now know that *Megaloolithus* is the most common dinosaur egg-type in the Upper Cretaceous of South-central Pyrenees (Tab.1), representing more than 90% of the oological record. At least, this group of fossil eggs could be represented by four to six oospecies (see Vianey-Liaud and López-Martínez, 1997; Escuer *et al.*, 2006; Vila *et al.*, 2011, but see Sander *et al.*, 1998; Peitz, 2000a, b), which can be grouped in three egg assemblages (Vianey-Liaud and López-Martínez, 1997; Garcia and Vianey-Liaud, 2001b; Vila *et al.*, 2011). The attribution of *Megaloolithus* to sauropod titanosaurs was reinforced with the discovery of embryos inside megaloolithid eggs in Argentina (Chiappe *et al.,* 1998). These dinosaurs excavated an elongated hole on the ground (Vila *et al.*, 2010c) and incubated their eggs underground (Deeming, 2006; Jackson *et al.*, 2008). But, this is only a partial view of the whole history and the oological record attributed to sauropods. For this reason, in following chapters, we will perform an overview of the oological record attributed to sauropodomorph. We will also show the role of Pyrenean record in the study of the paleobiology of dinosaurs.

Localities	Sites	Type of record	References
Noguera (Lleida Province)	Fotllonga-6	Eggshells	Vianey-Liaud and López-Martínez, 1997; López-Martínez *et al*, 2000
Pallars Jussà (Lleida Province)	Abella; Basturs-1 and 2; Biscarri; Faidella; Suterranya-1	Clutches and eggs	Lapparent and Aguirre, 1952a,b; Lapparent, 1959; Kohring, 1989; Moratalla, 1993; Sanz *et al*, 1995; Ardèvol and Krauss, 1991; Sander *et al.*, 1998; Ardèvol *et al.*, 1999; López-Martínez, 2000; López-Martínez *et al*, 2000; Bravo *et al*, 2000
	Barranc de la Munya; Moror; Sant Romà; Talarn; Els Nerets; Orcau; Abella; Fontllonga; Montrebei	Eggshells	Rosell, 1967; López-Martínez, 2000
Coll de Nargó Syncline (Alt Urgell, Lleida Province)	Coll de Nargó; Pinyes; Els Enserris; Sallent Poble; Santa Engràcia	Clutches and eggs	Rosell 1967; Plaziat 1972; Erben 1979; Sander, 1989; Peitz, 2000 a,b; Lòpez-Martínez 2000; Escuer *et al.* 2003, 2006; Vila *et al.* 2006; Sander *et al.* 2008; Jackson *et al.* 2008; Vila *et al.* 2010
Vallcebre Syncline (Berguedà, Barcelona Province)	Font del Bullidor; Fumanya Nord; Fumanya Sud; Mina Tumí; Les Quijoles; Els Terrers	Clutches and eggs	Aepler 1967; Peitz 2000; Galovart *et al.* 2002; Bravo *et al.* 2005; Fortuny *et al.* 2007; Vila *et al.* 2010, 2011
	Peguera-1; Sant Julià; Sant Corneli; Torrent de l'Esdavella; Coll de Jou	Eggshells	Bravo *et al.* 2005; Vila *et al.* 2011

Table 1. Localities with oological remains of megaloolithid eggs in Southern Pyrenees.

Chapter 2

GEOGRAPHICAL AND GEOLOGICAL SETTINGS

The Pyrenees is a range of mountains in southwest Europe that constitutes the natural border between France, in the North, and Spain, in the South. This mountain range extends for 430 km in longitudinal direction; from the Bay of Biscay, in the West, to the Mediterranean Sea, in the East. It separates the Iberian Peninsula from the rest of Europe (Fig. 1A).

2.1. GEOGRAPHICAL SETTINGS

In Catalonia (Northeastern Iberian Peninsula), the Upper Cretaceous fossiliferous outcrops that contain remains of dinosaur eggs and eggshells are located at the foothills of the Pyrenees, also known as the South Pyrenees. This fossil record is distributed in four Catalan administrative regions called “comarca”: Noguera, Passars Jussà, Alt Urgell (all three in Lleida Province) and Berguedà (Barcelona Province) (Fig. 1B). The number and geographical location of fossiliferous sites within each “comarca” depends on the situation of the Upper Cretaceous outcrops (Fig. 1C, D).

Pallars Jussà is the area that presents the most of the oological remains, with more than 20 fossil egg-sites distributed throughout this zone. The Vallcebre area, located in the Northern part of Berguedà, has yield several egg-sites scattered around the Vallcebre Syncline. A similar number of sites are concentrated in a small area near villages of Coll de Nargó and Sallent, in the southern part of Alt Urgell, which is known as Pinyes nesting area. Comparatively with other areas, Noguera has provided very few and scattered egg-sites, but in contrast, they are among the richest in oological diversity.

2.2. GEOLOGICAL SETTINGS

Pyrenees formed as consequence of continental collision between Iberian and European tectonic plates during the Late Cretaceous to the Early Miocene (Muñoz, 1992). This collision produced the deformation of the sedimentary basins deposited during the Mesozoic, which take place during an extensive tectonic period. Pyrenees extends from Cantabrian platform, in the west, to Provence region, in the east, with a length of 1500 km.

A Paleozoic basement constitutes this mountain chain. This basement was deformed during the Variscan Orogeny, and a sedimentary cover, developed a belt of folds and thrusts. Traditionally, Pyrenees has been subdivided in three main zones, on the basis of their geographical and geological conditions: the North Pyrenean Zone, the Axial Zone and the South Pyrenean Zone.

The study of present thesis has been developed in the South Pyrenean Zone, in the Iberian side, even many comparisons involve the North Pyrenean Zone, in the french side.

The South Pyrenean Zone is composed of a serial of allochthonous units that can affect materials from the basement and the cover (lower thrust sheets), or only from the cover (upper thrust sheets) (Muñoz *et al.*, 1984). Three main upper thrust sheets can be distinguished. They are, from North to South: Bòixols-Sant Corneli, Montsec and Marginal ranges. However, in the eastern part of Pyrenees, it can be identified two more thrust sheets named Pedraforca and Cadí (Vergés and Muñoz, 1990).

Each Upper Cretaceous basin studied in this thesis is located in a different "Comarca" and placed in a different thrust sheet. Thus, Àger Basin (Noguera) is located in Marginal range thrust in, while the Tremp (Pallars Jussà) and the Coll de Nargó (Alt Urgell) Synclines are situated at the top of the Montsec thrust and the Vallcebre Syncline (Berguedà) is contained in the Cadí thrust.

2.2.1. Uppermost Cretaceous continental deposits in South-Pyrenean zone: Generalities

Continental dinosaur eggs-bearing sediments from the Upper Cretaceous of the South Pyrenean Zone are concentrated in the Arén Sandstone Fm. and in the Tremp Fm., also known as Garumnian facies (Leymerie, 1862). This last terminology was firstly recognized in the Coll de Nargó Syncline (Leymerie, 1862), and later in the Vallcebre Syncline and Isona (Tremp Basin) (Vidal, 1871, 1874, 1875, 1921).

Those materials were deposited following a regressive trend of sea level in the Central Pyrenees, which took place near the Campanian-Maastrichtian boundary. This left some places of the basins under continental conditions (Rosell *et al.*, 2001). During the Campanian, Pyrenean basin was under shallow marine conditions, which allowed the development of a big deltaic system. First step of the regression trend was the placement of muddy tidal flats, palustrine areas and swamp zones with accumulation of vegetal matter. At the end of the Maastrichtian, this regressive trend was stronger in the eastern part of the basin, allowing the development of fluvial and alluvial systems. Later, it was generated a system of lakes in the most depressed points of the basin. Finally, a new tectonic phase allowed a new development of fluvial and alluvial systems (Rosell *et al.*, 2001).

Oological record of dinosaurs from the Upper Cretaceous of Southern Pyrenees come from two geological units, the Arén Sandstone Fm. and the Tremp Fm., even they are rare in the first one and very common in the second one.

Geologicaly, the Campanian-Maastrichtian Arén Sandstone Fm. (Mey *et al.,* 1968) represents beach, barrier-island systems and deltaic deposits, which are mainly composed of quartz grains and show medium- and large-scale cross-bedding (Riera *et al.*, 2009). The transition between the Arén Sandstone Fm. and the lowermost part of the Tremp Fm. is represented by a diachronic interfingering of strata (Souquet, 1967; Liebau, 1973). This diachronic character in the transition between both formations implies that the uppermost part of the Arén Sandstone Fm. can been dated as Late Campanian as Late Maastrichtian in age, depending on the geographical position of studied area.

The Tremp Fm. is present in the Montsec, in the Marginal ranges thrust and in their equivalents of the Pedraforca and Cadí thrust. The lower part of the Tremp Formation can be informally divided into the following three units (*sensu* Rosell *et al.*, 2001), from the base to the top: the “Grey unit”, the “Lower Red unit” and the “Vallcebre Limestones” (see Riera *et al.*, 2009). This last unit is Palaeocene in age, based on charophytes associations (Feist and Colombo, 1983; López-Martínez *et al.*, 2006). Dinosaur eggs and clutches are found in the two most basal units. Geological composition and paleoenvironmental inferences will be detailed in next paragraphs.

1. Grey unit - This unit is mainly formed by grey mudstones with abundant invertebrate remains such as bivalves, ostracods and gastropods. This sediment could be intercalated with limestone with charophytes and ostracods, and sandstones. The grey unit has been interpreted as variable salinity *lagoon* deposits, located near barrier-island systems, represented by the Arén Sandstone Fm. This *lagoon* would change gradually from tidal flat to continental swamp areas (Ardèvol *et al.* 2000; Rosell *et al.*, 2001). In those swamp areas, it would occur an abundant accumulation of vegetal material, producing a high amount of coal. This unit is dated as Lower Maastrichtian in age, based on its faunal content (Rosell *et al.*, 2001).

2. Lower Red unit - Composed of red mudstones, intercalated with sandstone and paleosoil levels. The Lower Red unit exhibits a base with oncolite levels and a top consisting of coarse-grain sandstone and microconglomerates levels, which have a long lateral continuity. These upper detritic levels could contain vertebrate fauna remains, mainly consisting on dinosaur bones and they are known as "Areniscas con reptiles" (Masriera and Ullastre, 1983; Ullastre and Masriera, 1983). The Lower Red unit has been interpreted as alluvial and fluvial deposits of a flood plain, with intercalations of fluvial channels of braided and meandering type, and lacustrine-palustrine limestones (Díaz Molina, 1987; Krauss, 1990; Cuevas, 1992; Rosell *et al.*, 2001). It is dated as Maastrichtian (Rosell *et al.*, 2001). The K-T boundary is located somewhere near the top of the Lower Red unit, sometimes immediately above the Vallcebre limestones.

3. Vallcebre limestones and laterally equivalences – This unit is formed by micritic limestones with charophytes and *Microcodium* at the top of the strata, and they have been interpreted as ephemeral lakes placed near the coastal edge (López-Martínez *et al.*, 2006). These units have been dated as Danian in age (Rosell *et al.*, 2001)

An upper stratigraphic unit can be identified within the Tremp Formation, known as "Upper Red unit". It is constituted of dark-reddish mudstones, sandstones and conglomerates. It can contain oncolites and *Microcodium* in its upper part. It has been interpreted as fluvial an alluvial systems formed during Paleocene (Rosell *et al.*, 2001). However, it is difficult to date continental deposits of the Tremp Fm., because they lack of useful elements to make this task. Even so, the "Grey unit" is rich in these elements, such as charophytes (Feist and Colombo, 1982), foraminiferous (Caus and Gómez-Garrido, 1989), ostracods (Liebau, 1973), molluscs (Liebau, 1973; Pons, 1977; Vicens *et al.*, 2004) and pollen (Médus *et al.*, 1992), helps dating this units.

Four sedimentary basins have been treated in this thesis (Àger, Tremp, Coll de Nargó and Vallcebre). Although all these basins basically record same sedimentological process, some differences can be observed between them, sometimes in facies contain, sometimes in the thickness of these facies.

2.2.2. Àger Syncline

In this area, the Tremp Fm. is 700 meters thick. Its base is in contact with the Limestones of Les Serres Fm. (Souquet, 1967), which is equivalent to the Arén Sandstone Fm. This calcarious formation is composed of bioclastic calcarenites and mudstones with rudists and foraminiferous. It is dated as Campanian-Maastrichtian

(Souquet, 1967; Caus and Gómez-Garrido, 1989).

The Tremp Fm. has been largely studied in this area, especially in Fontllonga section. There are many works on stratigraphy (Rosell and Llompart, 1988; Colombo and Cuevas, 1993; López-Martínez et al, 1998, 2006, among others), invertebrate faunas (Galbrun *et al.*, 1993), flora (Médus *et al.*, 1988; Médus and Colombo, 1991; López-Martínez *et al.*, 1999, among others), geochemistry (López-Martínez *et al.*, 1996, 1998; Domingo *et al.*, 2007) and on dinosaurs eggs (Vianey-Liaud and López-Martínez, 1997; López-Martínez, 2000). The age of this established at the Lattes Campanian, because the base of the Grey Unit falls in the magnetocrhone C32n (*sensu* Gradstein *et al.*, 2004).

The K-T boundary position in Àger Synclyne has been established between the top of the Lower Red unit and the base of the Vallcebre Limestones, coinciding with the absence of dinosaur record and the presence of *Microcodium* (Llompart and Kraus, 1982). These observations are coherent with the magnotostratigraphic results obtained by Galbrun *et al.* (1993), which recorded the C29r chron at the top of the Lower Red unit, and with the chemostratigraphic studies conducted by López-Martínez *et al.* (1998).

2.2.3. Tremp Basin

Tremp basin has been largely studied for more than a hundred years (Vidal, 1872, 1921; Dalloni, 1930; Bataller, 1958, 1959, 1960; Liebau, 1967; Rosell, 1967; among others). In this basin, the Tremp Fm. is overlapping and interfingering with the Arén Sandstone Fm. (Liebau, 1967; Díaz-Molina, 1987; Krauss, 1990; Ardèvol *et al.*, 2000). In this sector, the Arén Sandstone Fm. has been interpreted as shore deposits, barrier-island systems and delta deposits (Ghibaudo *et al.*, 1974; Nagtegaal *et al.*, 1983; Díaz-Molina, 1987; Mutti and Sgavetti, 1987). On the other hand, the Tremp Fm. shows high variability of deposits and thickness (Rosell, 1967; Puigdefàbregas and Souquet, 1986; Ardèvol *et al.*, 2000; Simó, 2004).

The age of the lowermost unit, the Grey unit, is widely accepted as Early Maastrichian, based on different biostratigraphical studies (Liebau, 1973, 1984; Pons, 1977, 1982; Feist and Colombo, 1983; De Porta *et al.*, 1985). However, data reported by Gradstein *et al.* (1995) suggest that previous sediment materials assigned to Early Maastrichtian are, indeed, Late Campanian in age. This new interpretation agrees with new stratigraphical and biostratigraphical studies (Ardèvol *et al.*, 2000; López-Martínez *et al.*, 2001; López-Martínez, 2003; Vicens *et al.*, 2004), which propose that the lowermost materials of the Tremp Fm. belong to the Upper Campanian. Concerning the K-T boundary position, this is placed near the base of the Vallcebre Limestones or lateral equivalents (Feist and Colombo, 1983).

In the western part of the Tremp Basin, in the Noguera sector, the age of the Tremp Fm. is quite different

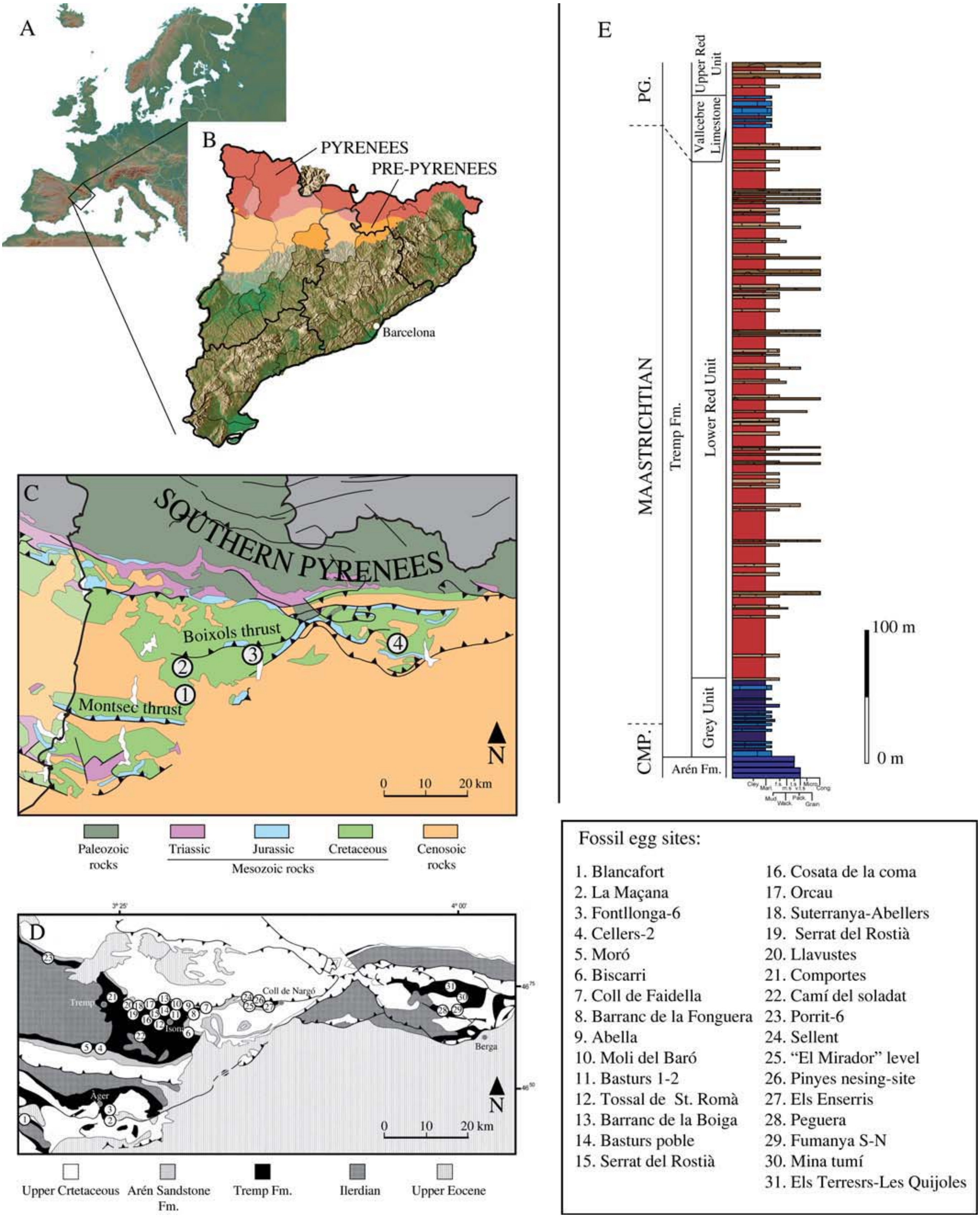

Figure 1. Geographical and geological settings. (A and B) Geographical map showing the location of the studied area. (C) Geological map of Southern Pyrenees of Mesozoic outcrops and location of studied basins. 1-Àger Syncline, 2-Tremp Basin, 3-Coll de Nargó Syncline, and 4-Vallcebre Syncline. (D) Geologycal map with location of main egg-sites. The number of each site is correlated with the list beside. (E) Lithostratigraphical section of the Tremp Fm. from Coll de Nargó Syncline as example of the Upper Cretaceous sediments.

from the eastern sector. According to magnetostratigraphical studies of Oms and Canudo (2004) and Pereda-Suberbiola *et al.* (2009), the Lower Red unit is compressed between C30n and C29r chrones, which belong to the upper part of the Maastrichtian. Thus, the Arén Sandstone Fm, the Grey unit and the lowermost part of the Lower Red unit are dated as belonging to the C30n magnetochrone.

2.2.4. Coll de Nargó Syncline

As we pointed out despite the high amount of works performed on Garumnian facies only few studies have been performed in Coll de Nargó Syncline (Baudrimont, 1961; Willems, 1985; Ullastre and Masriera, 2006).

In this area, the Tremp Formation includes coastal and continental deposits, encompassing from the Late Campanian to the Late Paleocene. It is generally located at the top of the Arén Sandstone Formation (Mey *et al.*, 1968; Willems, 1985). Most of the dinosaur-bearing outcrops are associated with the boundary of these two formations, and are often found in peri-tidal marls and in lutitic tidal flats (Díaz-Molina, 1987; Vianey-Liaud and López-Martínez, 1997; López-Martínez *et al.*, 2001). In the uppermost part of the Tremp Fm. it is often difficult to distinguish between the Mesozoic and the Cenozoic strata because of the paucity of fossil remains with chronostratigraphic values (Bataller, 1958, 1959; Liebau, 1973; Feist and Colombo, 1983; Médus and Colombo, 1991 Galbrun *et al.*, 1993).

The basal “Grey unit” is clearly exposed in Pinyes nesting site. It is characterised by 60 m of grey lutites, limestones and lignite layers interfingering the Arén Sandstone Formation (Díaz-Molina, 1987; Cuevas, 1992; Ardèvol *et al.*, 2000). Eggshells, clutches, few dinosaur footprints, ostracods, gastropods, charophytes and plant remains are found in this unit. These sediments were deposited in lagoonal or lacustrine-palustrine environments (Díaz-Molina, 1987; Cuevas, 1992). In this area, a gradual transition between the Lower Garumnian and the Middle Garumnian is noted (*sensu* Rossel *et al.*, 2001).

The middle “Lower Red unit” is formed by red clays, sandstones and conglomerates. It has a total thickness of 500 m. The red clays and marls are dominant in this section, although sandstones increase towards the top. The bioturbation is extensive in the marl levels, and hardened levels show many root casts and carbonated nodules that have been interpreted as calcimorph type palaeosoils (Díaz-Molina, 1987; Cuevas, 1992; Cojan, 1999). Two main bioturbation types can be observed in these levels: 1) meniscate bioturbation in section, with *Spirographites ellipticus* fully integrated into the sediment and associated with terrestrial arthropods (Mayoral and Calzada, 1998) and 2) non-meniscate bioturbation, where the casts can be clearly detached from the sedimentary rocks and interpreted as traces of plant roots in palaeosoils developed in mangrove-like swamps (Plaziat, 1972, 1981; Díaz-Molina, 1987). The dinosaur eggs and clutches found in these palaeosoils are well conserved given their resistance to erosion, because of their higher carbonate content. The most of the lenticular sandstone bodies, showing ripple cross lamination, and lateral accretion point bars, represent the sedimentary activity of channelized flows. Thin conglomerate and microconglomerates beds display numerous dinosaur eggshell fragments. A detailed description of the sedimentological facies of this unit was reported in Bravo *et al.* (2000) and in Vila *et al.* (2010a). The facies association suggest that the "Lower Red unit" consists of fluvial deposits, whereas the lutitic materials make up the floodplain environment. The calcimorph soils were originated during quiet periods between successive floodings (Plaziat, 1981; Cojan, 1999). The sandstones and conglomerates correspond to channel lag deposits, while sandstones with parallel lamination and antidunes (in some cases they can transport big clasts) suggest a high hydraulic regime flow discharge. The meander bars indicate a relatively low energy one. The multiple channel systems (Díaz-Molina, 1987) are well developed and widely displayed in the studied area.

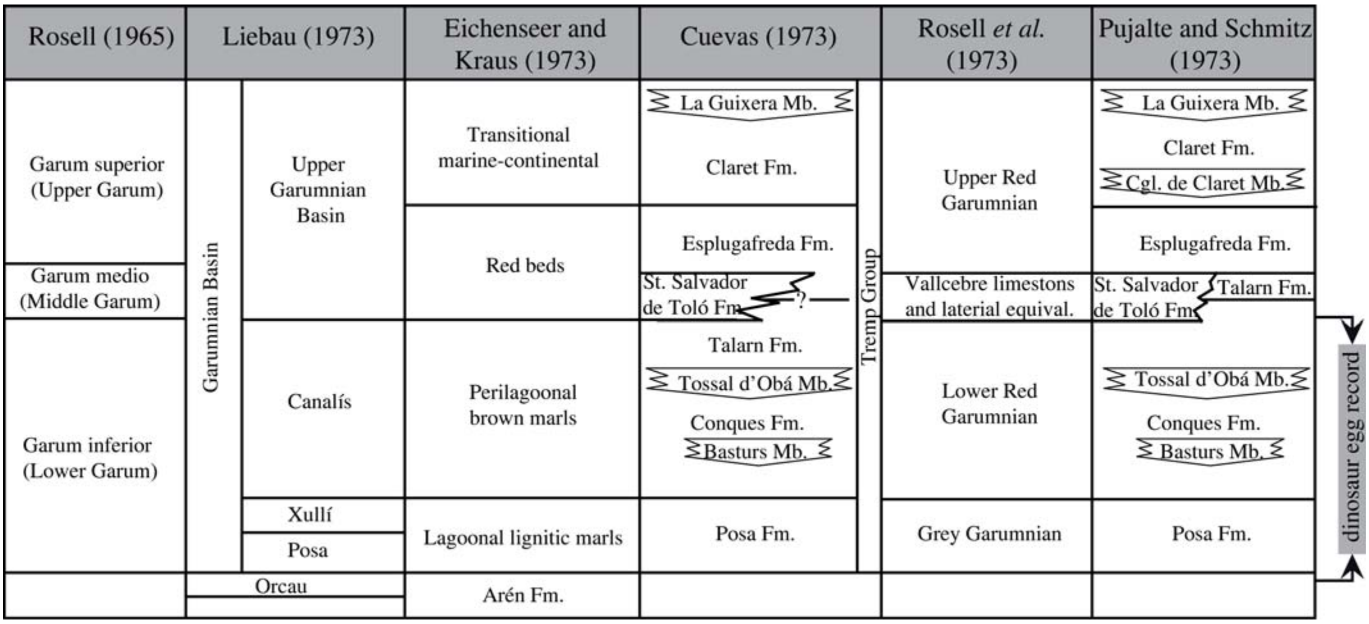

Figure 2. Lithostratigraphical subdivision on the Tremp Fm. in the Tremp Basin according some authors (modified from Riera, 2010).

2.2.5. Vallcebre Syncline

Although no extensive study has made on the oological material of Vallcebre Syncline in this PhD thesis, its fossil record is well represented in this area. It includes eggs, eggshells (Bravo et al., 2005; Vila et al., 2011) and the data that has been included on it. For this, it will only summarize here some data about the Tremp Fm.

In Vallcebre Syncline, the Tremp Fm. is 800 meters in thickness, 500 m of which are Late Cretaceous in age (Oms *et al.*, 2007). As occur in other basin, the Tremp Fm. is overlapping the underling geological unit, Terradets Limestones Fm., which is equivalent to the Arén Sandstone Fm. This formation is composed of marine material with *Hippurittes radiosus*, which is characteristic of the Late Campanian (Vicens, 1992; Vicens *et al.*, 2004). The Grey unit and the Lower Red unit are mainly Maastrichtian in age (C32n.1n to C29r) (Oms *et al.*, 2007), but it is no discarded that first meters of the Tremp Fm. could belong to Campanian. The K-T boundary would be placed between the upper part of the Lower Red unit and the base of Vallcebre Limestones (Oms *et al.*, 2007), which have been dated as Paleocene in age, according to the presence of *Dughiella bacilaris* charophite (Feist and Colombo, 1983), and to magnetostratigraphic results (Oms *et al.*, 2007).

Chapter 3

MATERIAL, METHODS AND PARATAXONOMY

Several techniques have been utilized for the study of the egg and eggshell material including: binocular magnifier, scanning electron microscopy and transmitted light microscopy for eggshell structure (Hirsch, 1983; Hirsch and Packard, 1987) and x-ray diffraction for crystal composition (Cain and Heyn, 1964).

3.1. MATERIAL AND METHODS

3.1.1. Acquisition of studied material

Previously to any type of analysis or lab study it was necessary to collect the studied oological material. This acquisition was obtained after fieldwork prospection and collection of samples, which have been coursed during the three years of this thesis project.

3.1.1.1. Sampling in Coll de Nargó (Alt Urgell)

Most of the eggshell samples have been recovered from *in situ* eggs and clutches distributed along 20 stratigraphic levels at Pinyes nesting site (Fig. 3). First, more than 150 eggshell fragments from 20 clutches distributed along consecutive levels of whole stratigraphical section of 370 m were sampled (IPS-58994 to IPS-59015). Additionally, three different horizons were laterally sampled (see also Fig. 2): the first horizon is located at 22 m from the base of the stratigraphic log, where 31 eggs have been found (IPS-59073 to IPS-59104); in the second horizon (at 190 m), 33 points represented by isolated eggs and clutches were sampled and 86 eggshell fragments were recovered (IPS-59017 to IPS-59050); at the last horizon (at 198 m), 22 points were sampled and 87 eggshells fragments were recovered (IPS-59051 to IPS-59072). Isolated eggshell fragments

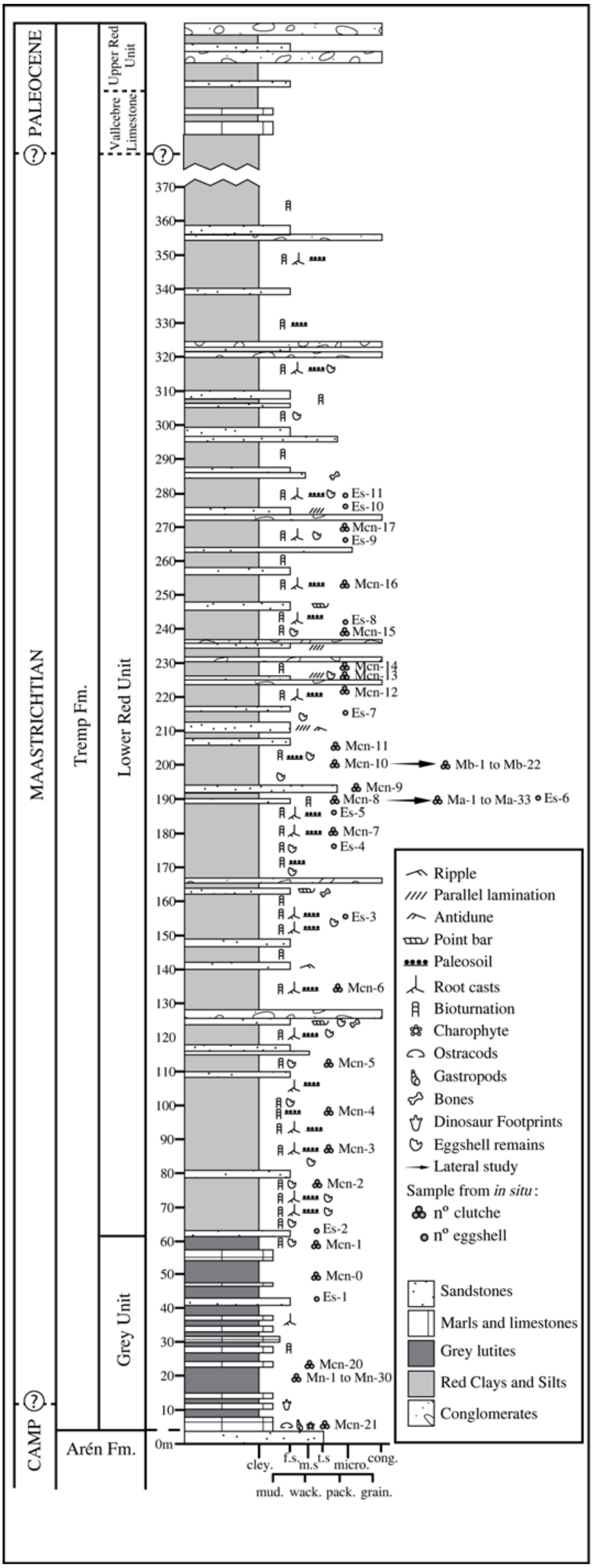

Figure 3. Stratigraphic log as an example of the Tremp Fm. in the Coll de Nargó Syncline and showing the position of the eggshells samples.

sampled from many consecutive stratigraphical levels completed the sampling (IPS-59105 to IPS-59115). Some of this material was previously referred in Escuer *et al.* (2006). A clutch containing 28 eggs (Vila *et al.*, 2010 c) was excavated near the sample IPS-59080.

3.1.1.2. Sampling in Àger and Tremp basins (Noguera and Pallars Jussà)

Up to 3000 eggshells from the Upper Cretaceous of Catalonia were recovered. Additionally, comparative oological material is obtained via particular donations or given by paleontological institutions. All the material is housed in the collection of the Institut Català de Paleontologia Miquel Crusafont, excluding those from La Massana outcrop, which was firstly collected by the study of charophytes (Villalba-Breva, per. com.) and housed in the department of Estratigrafia, Paleontologia i Ciències Marines of Universitat de Barcelona (see table Appendix I).

During the last three years, 282 sampling sacks were collected in these basins, with a total amount of 5600 kg of sediment, were collected. Then, this sediment was washed and sieved for obtaining the fossil material. The used screens had a mesh light of 1.4, 0.85 and 0.5 mm of diameter, which is the best interval to obtain eggshell fragments. Triage of samples was made using Leica® M60 binocular lent (0.63X to 4.0X). During this process, a preliminary classification of fossil eggshells was made, based on the outer ornamentation of the shells. The processing of this material is very slow, so it has only been possible to work with about 1130 kg of sediment, about the 20% of the total collected.

3.1.2. Preparation of fossil eggs and eggshells

Well-preserved eggshell fragments were sorted initially into separate morphotypes by examination of their outer surface ornamentation. A Leica® MZ16 binocular magnifier and Leica® Application Suites 2.8.1 software was used for examination and analysis. The thicknesses were measured using Vernier's calipers. Selected fragments were ultrasonically cleaned, rinsed in distilled water, and air dried. It is important to note that many eggshells had been covered from sediment or hard calcite concretions. Traditionally, the techniques used in the cleaning and preparation of fossil eggshells were based in the application of organic acids (i.e. Formic and Acetic acids) when matrix was rich in carbonate (Hirsch and Packard, 1987; Mikhailov, 1991, 1997; Zelenitsky, 1995; Carpenter, 1999). This constitutes a problem, because these acids attack, in the same way, the matrix carbonate and the eggshell, producing significant damages in the structure of the eggshells. These damages avoid an optimal study of the material, plus they could destroy the features of the eggshells. Val *et al.* (2010) proposed new methods for clean fossil eggshells, specifically dinosaur eggshell.

In the Late Cretaceous deposits of South Pyrenean basins, as is stated above, the eggshells are imbedded within highly carbonated matrix. For the properly clean of the eggshells, it was performed a study using different types of chemical treatments and analyzing their effects using scanning electron microscopy. Preliminary results are listed below (Table 2, and see also Fig. 4).

According to the obtained results, KOH and SHMP 30% are the best treatments for the preparation of fossil eggshells, although they do not clear the entire sediments adhered in the shell, they slightly degrade the shell surface.

3.1.3. Scanning Electron Microscopy (*SEM*)

Scanning Electron Microscope (*SEM*) is a type of electronic microscopy that uses a beam of electrons for composing an image. It has great depth of field, allowing focus a large area of simple. It has a resolution between 4 and 20 nm, depending on the type of microscope.

In oology, this technique is applied to the study of the ultrastuctural elements of the eggshell, such as the crystalline morphology of shell units, which reveals fine composition of the shell. Furthermore, it can also be used for the observation of the microstructural characters (i.e. pore canals, shell unit, wedges, basal caps…).

The eggshell fragments were mounted on aluminum stubs using double-sided carbon tape, when they

TREATMENT	EFFECTS
EDTA 5%	**Slight to moderate** - moderate modification of ornamental nodes. Sample still with sediment adhering.
EDTA 5% + NaOH 4%	**Strong**– strong modification of external ornamentation, but distinguish limit between shell units.
HCL 30%	**Strong**– outer surface appears nearly smooth, disappearance of ornamentation.
KOH	**Slight** - slight modification of ornamental nodes. Sample still with sediment adhering.
DMSO 5% for 1 week	**Slight** – No observable modification of external ornamentation. Sample still with sediment adhering.
DMSO 5% for 2 month	**Slight** – slight modification of external ornamentation.
SHMP 30%	**Slight** – slight modification of external ornamentation. Sample still with sediment adhering.
SHMP 50% + Waller Method	**Total** – complete removal of external ornamentation.
Waller Method	**Moderate** – large modification of external ornamentation. Sometime nodes appear corroded.

Table 2. Diverse treatment used in the preparation of fossil eggshells and their effects involving the degree of dissolution of the eggshell surface (in bold) and its implications.

were small and thin, or with silicone, when they were big and thicker. In order to view the inner, outer, and radial surfaces, the shell fragments were placed in different orientations. Specimens were examined and photographed using a ESEM Quanta 200 FEI, XTE 325/D8395 placed on the Scientific-Technical Services of the Universitat de Barcelona. Qualitative composition analyses on eggshells were conducted using a BSE detector at high and low vacuum.

3.1.4. Thin-section preparation

In optical mineralogy and petrology, as well as in oology, a thin section is a laboratory preparation of a sample for the use with polarizing petrographic microscope.

This technique is intended for the observation of microstructural characters of the eggshell (Fig. 5), which are useful for the classification of fossil material.

Eggshell fragments were embedded in resins that allowed curing. The mold was cut to expose a desired eggshell surface for thin sectioning; either a tangential or radial surface was prepared. This surface was lapped using 600 and 1200-grit crystallite diamond disks on a Bueheler polisher/grinder and polished manually using

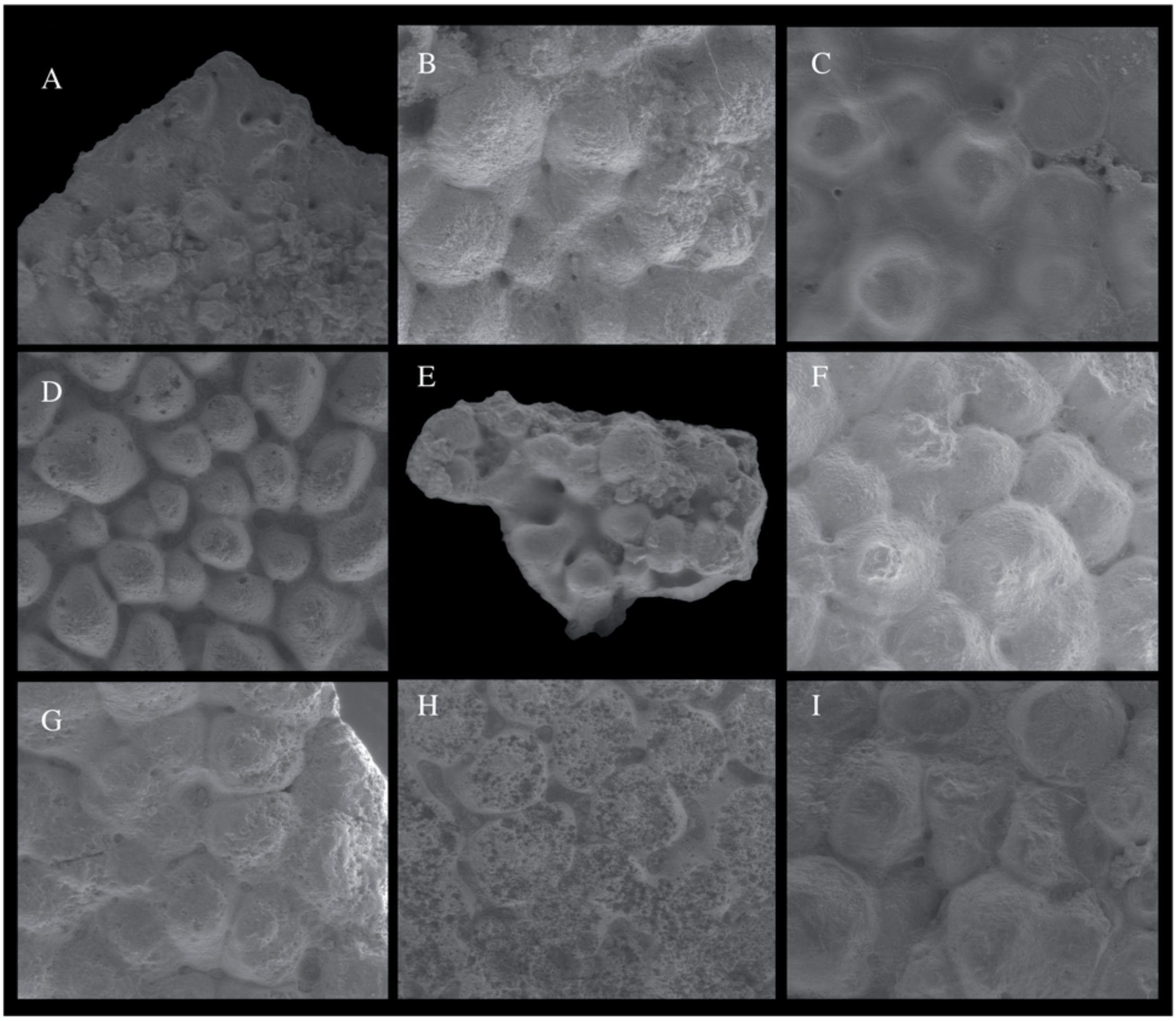

Figure 4. Results obtained in the preparation of fossil eggshells using A) EDTA 5%, B) EDTA 5%+NaOH 4%, C) HCL 30%, D) KOH, E) DMSO 5% for 1 week, F) DMSO 5% for 2 month, G) SHMP 30%, H) SHMP 50% + Waller Method and I) Waller Method.

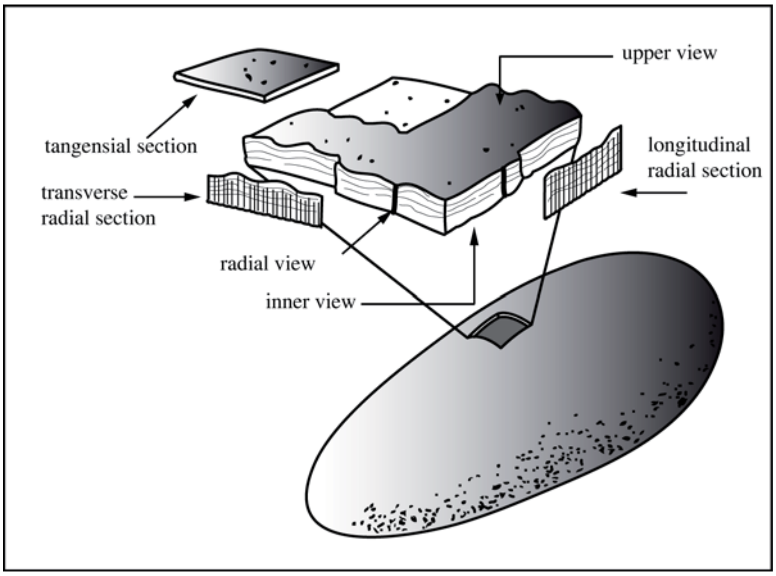

Figure 5. The principal topological terms concerning the egg and eggshell preparations. (modified from Sabath, 1991).

Bueheler micropolish (0.03 µm aluminum oxide). The polished surface was cold-mounted on a plain glass slide using Epotech 301 two-part epoxy. These slides were left to dry over a 24-hour period and then; they were resectioned on an automated Logitech re-sectioning saw.

Lapping was done by hand on a glass plate using 600 and 1000-grit silicon carbide until the desired thickness was obtained, usually 30-120 µm. A drop of glycerin and a glass cover slip were placed on the unpolished surface for microscopy examination. Thin sections were examined under ordinary light microscopy and polarizing light microscopy.

3.1.5. Descriptions

Systematic descriptions of the fossil eggshell are primarily based on the structural features observed under transmitted light microscopy and scanning electron microscopy. The egg and eggshell characteristics examined in this study, as well as the corresponding techniques utilized for their analysis, include: 1) egg size and shape; 2) outer surface ornamentation and pore patterns (scanning electron microscopy and dissecting microscope); 3) eggshell thickness (Vernier's calipers); 4) eggshell ultrastructure (scanning electron microscopy); and 5) eggshell histostructure (scanning electron microscopy and transmitted light microscopy).

The use of scanning electron microscopy and transmitted light microscopy complements each other in the identification of characteristics relating to eggshell microstructure. For example, eggshells ultrastructure is visible under scanning electron microscopy, whereas their histostructure (morphology and arrangement of shell units) is more apparent under transmitted light microscopy. Therefore, both techniques were utilized for the examination of the morphotypes of eggshells.

3.2. INTRODUCTION TO THE PARATAXONOMYCAL CLASSIFICATION OF FOSSIL EGGS

The study of fossil eggs is probably one of the most recent disciplines in vertebrate paleontology, although first remains are reported at the end of the 19th century. For a long time, the study of this fossil record consisted in a simple description of the size and shape of fossil eggs or of the ornamentation of their surface. They did not attend to microscopic characters. Apparently, all those remains were very similar and it was not necessary to name each new specimen. In fact, most of those scarce first findings were included under the name, *Oolithes*, which means “stone egg” (Buckman, 1859; Carruther, 1871). But other authors followed their own nomenclature (see Brandt, 1873). During decades, paleontologist continued using the same nomenclature, where the name of genus was fixed (*Oolithes*) and the name of the species varied depending on the egg shape (e.g. *O. spheroides* or *O. elongatus* (Young, 1954)) or shell thickness (e.g. *O. megadermus* (Young, 1959)). Hundred years after firts discoveries, Vialov (1972) introduced the name Veterovata (“old eggs”) in his principle of ichno-nomencalture, which included all fossil eggs and eggshells with a vertebrate and invertebrate origin (Mikhailov *et al.*, 1996).

The modern parataxonomical classification system was created after the approach made by the Russian paleontologist Victor B. Sochava (1969). He was the first to identify different structural morphotypes of eggshells based in the shape of pore canals and in the presence of diverse structural layers. Following that work, Zhao (1979) developed a parataxonomical system for dinosaur eggs using binomial nomenclature. The growing needs to put in order the increasing fossil record led to Mikhailov *et al.* (1996) to formalize the current parataxonomical classification for fossil eggs. According to this classification, equivalences with each taxonomical rang were established. They added the prefix “oo” to distinguish the egg species, genus, and family: oospecies, oogenus, and oofamily, respectively. Parataxonomy also uses the root “-oolithus” or “-oolithidae” within the genus and family name (e.x. *Megaloolithus*, *Elongatoolithus* or Prismatoolithidea, Spheroolithidae).

3.2.1. Eggshell structure

The amniota eggshell is composed of calcium carbonate and organic matter. Based on their composition, two main types of eggshell membranes can be recognized: 1) a shell membrane with variable amount of poor-organized calcareous matter and 2) a shell membrane with a calcium layer. In the first type of eggshell membrane, crystals float within the membrane or are mainly concentrated in the outer half of this membrane, as occur in some eggs of snakes and lizards. However, variations within these soft-shelled eggs can be identified, where calcium forms a crust or ornaments on the outer shell surfaces, as in other snakes and lizards, even it can be observed loosely organized columns interwoven with the organic fibers of the membrane, as in tuatara and bearded dragon (Hirsch, 1996).

In the second type of eggshells, calcareous matter can be poorly organized with loosely-abutting crystalline shell units, such as in sea turtles; better organized with tightly-abutting shell units, such as in snapping turtles; or well organized with interlocking shell units, as in rigid-shelled eggs of tortoises, some geckos, crocodiles, birds or dinosaurs.

The relationship between organic and crystalline matters and their organization makes easy to recognize each type of eggshell. This described nature allows its preservation in the fossil record. Soft and pliable-shelled eggs are mainly composed of organic matter, which start to desiccate shortly after the hatchling and later decays. Crystalline units of pliable shells are rarely recognized as an eggshell component after the organic matter decay, being easily disaggregated. For these reasons, this type of amniotic shell is difficult to be preserved in the fossil record. On the other hand, the hard calcareous structures of rigid-shelled eggs have more possibilities of to be preserved, fossilized and identified, because they are more stable and strong with an unalterable structure (Hirsch, 1996).

The abundance and diversity of fossil eggs and eggshells has raised problems for their identification and classification. These problems have emerged since the first attempts to create a comprehensive classification were made (Sochava, 1969, 1971; Zhao 1975, 1979; Erben *et al.*, 1979). The lack of diversity of fossil material available to individual workers, on the one side, and the limitations of techniques, on the other (Mikhailov, 1987), seem to be responsible of the inadequate morphological interpretations of some fossil eggshell remains (Mikhailov, 1997).

Different levels of biomineralization are adequately interpreted as structural levels of organization. One can distinguish between the macrostructural or textural, microstructural, ultrastructural and molecular levels (Barskov, 1988). Making a comparison between skeletal structure and eggshells, we could say that the macrostructue is referred to the “morphological unit” while microstructure (structural stratification of element) is regarded as the “tissue”. The ultrastructure and molecular interactions characterize more fundamental relations of the mineral and organic phases (Golubev, 1988). This nomenclature of structural levels can be applied to any morphological element (Mikhailov, 1997). But, from a practical point of view, we could distinguish two structural levels:

1) Macrostructural features or general morphology of egg and shell: egg shape and size is attached at this level; shell thickness; surface sculpture (ornamentation) and pore patterns. Some morphological features, such as egg size or shell thickness, can coincide in different ootaxa; thus,

they should be considered as subsidiary characters within taxonomical range (oofamily or oogenus level). One of the most important macrostructural characters is the ornamentation of eggshell, which can be present in three states: 1) smooth, 2) rough or 3) sculptured surface. However, in some types of eggs, (e.g. Prismatoolithidae and Elongatoolithidae) the ornamentation can change along the egg surface (Mikhailov, 1991, 1997). In fact, it seems that ornamental patter could be related to different growing patterns of shell units.

2) Histostructural features (commonly called "microstructure"; "eggshell unit macrostructure" in Mikhailov, 1991, 1997): all the observable characters on fractures and thin sections of the shell. This level includes the shell unit shape and size, pore canal system, morphology and structure of mammilla, prisms, wedges, columns, basal cap and basal plate group. Here, it is also taken into account the organic core and the ultrastructure of the eggshell, which can be: aragonite radial, calcite radial, tabular, radial-tabular or squamatic.

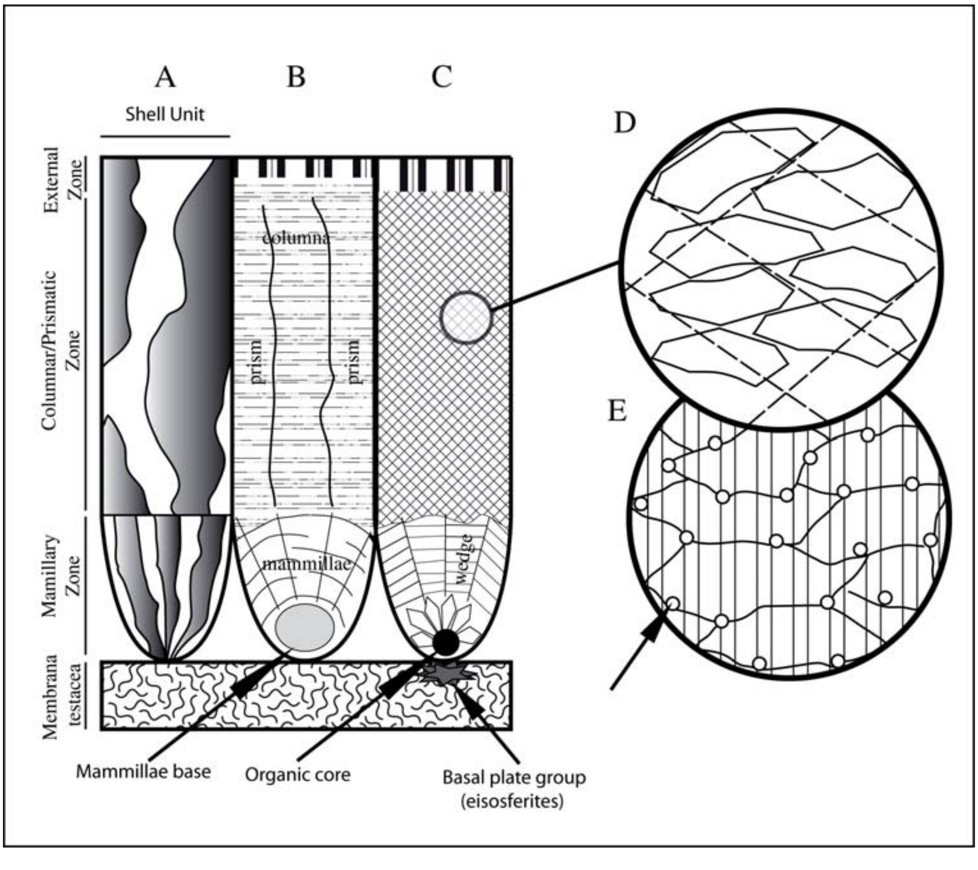

Figure 6. General terminology of eggshell structure based on avian eggshell. Sketch drawings of a real view seen in radial section, under Polarized Light Microscope (A), Light Microscope (B) and Scattering Electronic Microscope (C). D-E, squamatic ultrastructure at high magnifications; D, 'fish-bone pattern' superimposed on a pattern of the squamatic shell units; E, organic matrix consisting of large membranes, fine fibrils and vesicles. Arrow shows a vesicle. (redrawn from Mikhailov, 1997).

3.2.2. Terminology

The microstructure of the eggshell has been well studied for over a century. Von Nathusius (Von Nathusius (1887) translated by Tyler, 1964) examined avian eggshell and applied the terms spongy layer, mammillary layer, and cuticle to the various features that he recognized under a light microscope. Subsequent studies on eggshell resulted in an extension of this terminology (Romanoff and Romanoff, 1949; Tyler and Simkiss, 1959; Tyler, 1969; Becking, 1975; Mikhailov, 1987). Additionally, the analysis of both modern and fossil eggshell has unveiled an entire new aspect of eggshell structure and terminology (Sochava, 1969; Erben *et al.,* 1979; Grine and Kitching, 1987; Hirsch and Quinn, 1990; Mikhailov, 1991, 1992; Hirsch, 1994a). The introduction of many synonymous terms, in addition with the high diversity of eggshell structures, has complicated the nomenclature of the eggshell structure. All the researcher community should adopt a standardized system of nomenclature and terminology for the different eggshell characteristics.

In order to correctly apply the terminology, one must have an understanding of the 'basic types of eggshell organization' and their corresponding 'structural morphotypes'. Mikhailov (1991, 1992, 1997) discussed the characteristics of eggshell morphogenesis at the ultrastructural and histostructural levels (Fig. 6). He established the 'basic types of eggshell organization' and explained the correct application of Mikhailov's (1997) terminology of eggshell's structure.

For the purpose of simplifying, a single set of terminology, listed below, has been used throughout this thesis:

Accretion lines (growth lines, growing striation) - stratification of eggshell representing the concentric addition of shell layers.

Aragonite radial ultrastructure - ultrastructure composed of aragonite crystals radiating outwards from a central core; forming the shell units of testudoid-type eggshell.

Base of mammilla (basal spherolite) - apical portion of the mammilla that houses the organic core and abuts the eisospherite of the shell membrane.

Basal plate groups - ultrastructure composed of platy crystalline aggregates of discrete calcite crystals, situated in the uppermost fibers of the shell membrane; forms the eisospherites in ornithoid and dinosauroid eggshell. See also eisospherite.

Basic type of eggshell organization - a structural group established on the basis of the eggshell texture or sequence of subhorizontal ultrastructural zones.

Central core - spherical cavity in the base of the shell unit that houses the organic core.

Column (column, zone of column) - the upper columnar portion of the shell unit composed of prisms; applies to ornithoid neognathe and dinosauroid prismatic-type eggshell.

Continuous layer (single layer) - a homogeneous (shell units are non-distinct) histostructural layer that lies external and adjacent to the mammillary layer; applies to ornithoid ratite eggshell.

Eggshell texture - the sequence of subhorizontal ultrastructural zones within the eggshell.

Eisospherite (basal cap) - a crystalline body of platy elements, situated in the uppermost fibers of the shell membrane, abutting the base of mammilla.

Elongation index - The numerical value obtained by dividing the diameter of the long axis of the egg by that of the short axis.

Exospherite - the vertical shell unit composed of column and its subjacent mammilla.

External layer (external zone, vertical crystal layer) – zone of the external layer of the eggshell that is composed of vertical calcite crystals.

Histostructural layer- a subhorizontal zone or layer (i.e. prismatic layer, continuous layer, mammillary layer) within the eggshell that is composed of a specific type of subunits (i.e. prisms, wedges); refers to histostructure rather than ultrastructure.

Histostructure - the structure of the eggshell encompassing both the morphology and arrangement of the pore canals and shell units.

Macrostructure (superficial morphology) - the structure of the egg and eggshell encompassing the egg size, egg shape, shell thickness, outer surface ornamentation, and pore patterns.

Mammilla (basal cone, cone, mammillary process) - the cone-shaped, inner portion of the shell unit composed of wedges and radiating calcite crystals. The term “mammilla” is mainly utilized for dinosauroid prismatic-type eggshell, in reference to the innermost portion of the shell unit, but it is also applied as synonymous of the most basal part of shell units in dinosauroid spherulitic-type eggshells.

Mammillary layer (cone layer, mammillary zone, papillae layer) - the innermost histostructural layer of the eggshell that is composed of mammillae; applied to ornithoid (avian) eggshell.

Microstructure - a term that includes both the eggshell histostructure and ultrastructure.

Organic core (organic nucleus, mammillary core, primary spherite, spherite body) - the accretionary particle housed in the base of the shell unit that serves as a nucleation point for shell unit formation.

Ornamentation (sculpturing pattern) - the pattern of ornamentation on the outer eggshell surface. The various types of outer surface ornamentation are listed below.

Coaleseituberculate - coalescent nodes having no apparent orientation; derived from dispersituberculate.

Compactituberculate- a dense pattern of tubercles created by the roofs of the shell units.

Dispersituberculate - randomly dispersed isomorphic nodes.

Lineartuberculate - sculptural elements (ridges and nodes) are elongated and parallel the longitudinal axis of the egg.

Ramotuberculate - tubercles ramify, i.e. ridges and nodes are branch-like; derived" from linearituberculate ornamentation.

Sagenotuberculate - nodes and ridges are formed for the roofs of the shell units; and create a net-like sculpture pattern around the pore apertures.

Palisade layer - a layer composed of columns that display squamatic ultrastructure, lying external and adjacent to the mammillary layer; applies to ornithoid neognathe eggshell.

Pore aperture - the opening of the pore on the outer eggshell surface.

Pore canal (aeriferous canal, canaliculae) - A canal extending from the inner to the outer eggshell surface.

Pore pattern - the distribution of pore apertures on the outer surface of the eggshell.

Prism (prismatic unit) - a vertical subunit of the shell unit that forms the prismatic layer and palisade/continuous layer in dinosauroid prismatic and ornithoid eggshell.

Pore system- the network of pore canals throughout the eggshell (Fig. 7). The different types of pore systems are listed below.

Angusticanaliculate - pore canals are relatively straight and narrow, maintaining a constant diameter throughout their length. Mikhailov (1997) suggested that this type of pores is found in eggs laid in a dry environment.

Multicanaliculate - pore canals are relatively straight and slender, closely spaced and often branching. In eggs with this type of pores, gas exchange is high, restricting this egg type to humid environment (Mikhailov, 1997).

Obliquicanaliculate - pore canals rise from between the "mammillae" and cut obliquely through several shell units, having a fairly constant diameter. This type os pore canal is only known from some Jurassic dinosauroid prismatic-type eggshells.

Prolatocanaliculate - pore canals are irregular-shaped and change diameter throughout their length. They may be subdivided into faveocanaliculate, which have enlarged pore openings; and lagenocanaliculate, which are narrow pore openings. Eggs with this type of pores can be found in a great variety of environments (Mikhailov, 1997).

Rimocanaliculate - canals are narrow (slit-like) and shaped like a flattened funnel. This type canals co-occurs with angusticanaliculate and prolatocanaliculate pore system. The ostrich egg has rimocanaliculate pore canals, suggesting that dinosaur eggs with this type of canal laid their eggs is similar environmental conditions.

Tubocanaliculate - pare canals are similar to the angusticanaliculate type, except some canals have enlarged funnel-shape openings. In eggs with this type of pores, gas exchange is high, restricting this egg type to humid environment (Mikhailov, 1997).

Prismatic layer (prismatic zone) - the outer histostructural layer composed of interlocking prisms, lies external and adjacent to mamillary layer; applies to dinosauroid prismatic eggshell.

Radial section view (transverse section, lateral view) - a section or view perpendicular to the eggshell surface.

Shell unit - the basic structural unit that forms the eggshell. In the literature, the terms spherolith (= fan-shaped shell unit of dinosauroid eggshell) and exospherite (=shell units of ornithoid eggshell or shell units of dinosauroid eggshell) have been used by various authors. For these purposes, the term 'shell unit' is utilized to designate the basic structural unit, regardless of the eggshell type.

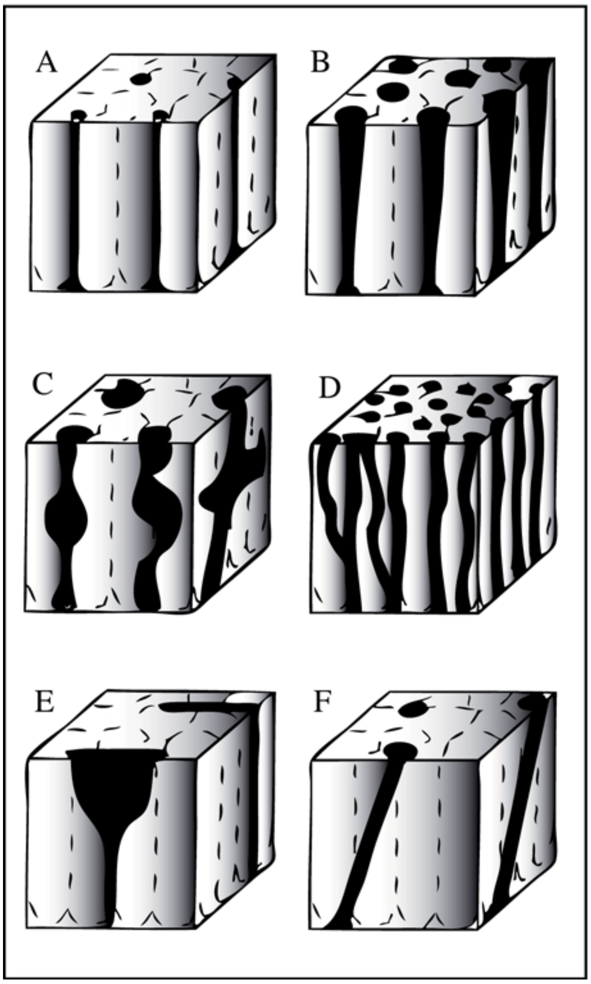

Figure 7. Types of pore system in amniotic eggshell. Schematic three-dimensional drawings, (A) angusticanaliculate; (B) tubocanaliculate; (C) multicanaliculate; (D) prolatocanaliculate; (E) rimocanaliculate and (F) obliquicanaliculate. (redrawn from Mikhailov, 1997).

Spherulitic - refers to the fine, radiating crystallites that comprise the shell units in

dinosauroid-spherulitie and testudoid-type eggshell.

Spongy layer - a general term for the continuous layer and palisade layer of avian (ornithoid) eggshell that displays squamatic ultrastructure.

Structural morphotype - a structural group established on the basis of eggshell ultrastructure and histostructure. A further subdivision of the basic type of eggshell organization for these structural morphotypes sees definitions below.

Subunit - The basic structural unit that forms the shell unit (i.e. prism, wedge).

Tangential section view - a section or view that is parallel to the eggshell surface.

Ultrastructure – “defines the shell unit as a tissue by its characteristics, its morphological configuration, and arrangement (mode of aggregation) of micron-sized (up to 20-30 μm) crystalline and organic elements aggregated a distinctive way into different zones within the shell units along the long axis” (Mikhailov, 1992, p.363).

Ultrastructural zone - a continuous subhorizontal zone within the eggshell that exhibits a specific type of ultrastructure (i.e. tabular, squamatic, calcite radial ultrastructures).

Calcite radial ultrastructure - ultrastructure composed of calcite plates radiating from an organic core that forms the base of the mammillae; applies to avian (ornithoid) eggshell.

Calcite spherulitic ultrastructure - ultrastructure composed of calcite crystals radiating outwards from a central core, forming the shell units of dinosauroid spherolitic-type eggshell.

Squamatic ultrastructure – ultrastructure in the continuous layer and palisade layers of ornithoid (avian) eggshell that is composed of squamatic (scale-like) aggregates.

Tabular ultrastructure - ultrastructure composed of tabular crystalline aggregate that is indicated by the occurrence of subhorizontal striations. It is apparent in the wedges of ornithoid eggshell, and in the wedges and prisms of dinosauroid prismatic eggshell. This may not represent ‘true’ ultrastructure, but rather the growth of the eggshell (Zelenitsky, 1995).

Wedge - a subunit of the shell unit that is wedge-like in longitudinal section and polygonal in transverse section.

Zone of prisms - a subhorizontal zone composed of prisms; applies to dinosauroid prismatic eggshell. See also prismatic layer.

Zone of radial calcite crystals - the ultrastructural zone composed of radiating calcite crystals; applies to ornithoid and dinosauroid spherulitic eggshells

Zone of squamatic aggregates - the ultrastructural zone composed of squamatic aggregates; applies to avian (ornithoid) eggshell. See also squamatic ultrastructure.

Zone of tabular crystalline aggregates - the ultrastructural zone that is composed of tabular crystalline aggregates. See also tabular ultrastructure.

Zone of vertical crystals - the ultrastructural zone composed of crystals oriented perpendicular to the outer surface; applies to avian (ornithoid) eggshell.

Zone of wedges - a subhorizontal zone composed of wedges; applies to crocodiloid, dinosauroid prismatic, dinosauroid spherulitic, and ornithoid eggshell.

3.2.3. Basic types and morphotypes of eggshell structures

Combining different macrostructural, microstructural and histostructural features, six basic structural types of hard eggshell of amniotic vertebrates have been recognized. In turn, it can be recognize different morphotypes of eggshell within each basic type of eggshell structure (Fig. 8).

Geckonoid basic type – Eggshell is composed by vertical fine and irregular crystals. It is no possible talk about “geckonoid shell units” because this type of eggshell lags nucleation centers. Outer surface is rather smooth but sometime shows large rounded nodes.

Testudoid basic type - Eggshell consists on a single ultrastructural zone of aragonite radial ultrastructure. Shell units are formed of spherulitic elements radiating from a central core. Outer surface in mainly smooth, sometimes rough and pore canals are narrow and straight (angusticanalitulate). Hirsch (1996) notes that it was possible to distinguish two morphotypes within testudoid basic type, depending on amount of calcium with compose the shell. This character controls the high/wide ratio of shell units and the interlocking between adjacent units.

Spheruflexibilis - individual shell units are wider than they are high, or as high as they are wide. Shell units loosely abut adjacent shell units.

Spherurigidus - shell units are higher than they are wide, and interlock with adjacent shell units.

Crocodiloid basic type – Eggshell is made up of tabular plates of calcite and loosely resemble the wedge zone of avian eggs. Shell units are also wedge in shape and often they are fused. There is no organic core at the base of the shell units, but rather an aggregation of calcite plates that serve as the nucleation site (basal plate group).

Dinosauroid spherulitic basic type – The shell consist of single ultrastructural layer and shell units are more or less fan shaped. Initially, the dinosauroid spherulitic basic type was suggested as having shell units composed of radiating wedges that display tabular ultrastructure (Mikhailov, 1992). The entire shell unit was apparently analogous to the wedge layer of the mammilla in ornithoid eggshell. Subsequent to this it was suggested that the ultrastructure, initially interpreted as tabular, is now speculative (Mikhailov, 1997). However, there are several variations in the morphology of shell units and pore systems within dinosauroid spherulitic basic type, which allow establish five structural morphotypes:

Tubospherulitic (also known as disctretispherulitic) – Well distinguished fan-shaped shell units form a compactituberculate ornamentation on the outer surface. The pore system is of the tubocanaliculate-type. This morphotype is exhibit by *Megaloolithus* egg type.

Filispherulitic - spherulitic crystals grow to form narrow prisms, which about adjacent prisms and create a network of crystalline “walls”. The pore system is of the multicanaliculate-type. Outer surface can show both smooth to compaticuberculate ornamentation. This structure is present in *Faveoloolithus* eggs.

Prolatospherulitic - structurally similar to the tubospherulitic morphotype. The shell units are fan-shaped, and tend to join at their lateral boundaries at 2/3 - 3/4 of the shell unit height. Prolatocanaliculate and rimocanaliculate pore systems are present in this morphotype. Outer surface could be sooth by is frequently sagenotuberculate (with ridges and nodes). *Spheroolithus* egg types show this morphotype.

Angustispherulitic – Similar to prolatospherulitic morphotype. Fan-shape sell units are strongly fussed with adjacent ones at 3/4 of the wall shell thickness. But differ from the precious morphotype in the pore system, being angusticanaliculate (very narrow canals) in angustispherulitic morphotype. This morphotype is attributed to *Ovaloolithus* egg type.

? Dendrospherulitic - a network of spherulitic crystals forms the inner wedges that grade into bundles of slender prisms at 1/6-1/3 of the shell unit height. A network of ramifying canals, produced by discontinuities within the shell structure, exists amongst the prisms. Outer surface is rather smooth or rough. We want note that dendrospherulitic morphotype is characteristic of particular theropod eggs type (*Dendroolithus* and *Dictyoolithus*). Recently, Jin *et al.* (2010) provided new information about eggshell of *Dictyoolithus*. They note shell units were composed of mamillary and prismatic zone, which are typical of dinosauroid-prismatic basic type (see below), but crystalline units lacked squamatic ultrastructure as commonly occurs in prismatic basic type. Similar condition has been observed in *Dendroolithus,* which is attributed to therizinosaurs (Manning *et al.*, 2000; Kundrát *et al.*, 2007). Shell units of *Dendroolithus* also are prismatic-shaped. According to our knowledge on theropod eggs, they might show dinosauroid prismatic or ornithoid morphotype. It suggests us that dendrospherulitic morphotype must be assigned to dinosauroid prismatic basic type.

Dinosauroid prismatic basic type- The eggshell consists of a single zone of tabular ultrastructure that comprises the inner zone of wedges (mammillary layer) and the outer zone of prisms (prismatic layer). The radiating wedges grade into the vertical prisms of the prismatic layer. Pore canals are narrow, straight or oblique. Outer surface is smooth or slightly rough, sometimes with dispersituberculate ornamentation.

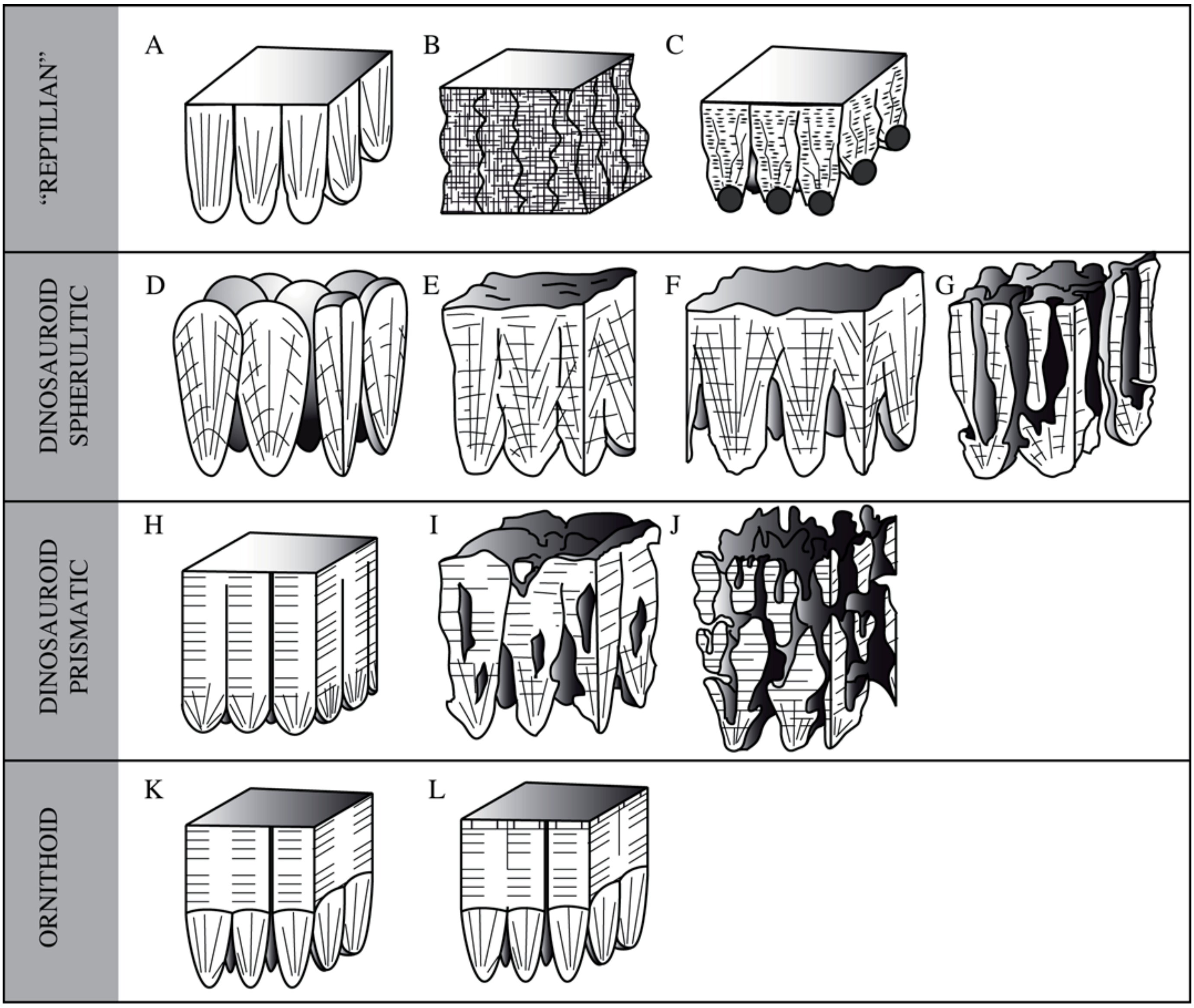

Figure 8. Morphotypes of eggshell structure in amniotic eggs. Schematic diagram of the basic shell units. (A) discretispherulitic (turtles); (B) crocodiloid; (C) geckoid; (D) discretispherulitic (Megaloolithidae); (E) prolatospherulitic (Spheroolithidae); (F) angustispherulitic; (Ovaloolithidae); (G) filispherulitic (Faveoloolithidae); (H) prismatic (Prismatoolithidae); (I) dendrospherulitic (Dendroolithidae); (J) dendrospherulitic (Dictyoolithidae); (K-L) ratite; (K), Elongatoolithidae; (L) Ratite.

Angustiprismatic/Obliquiprismatic - tall, narrow shell units interlock with adjacent units. The wedges of the inner mammillary layer grade into the prisms of the outer prismatic layer. The mammllary layer is approximately 1/7 - 1/2 of the entire shell thickness. Pore system is of the angusticanalicu1ate-type or obliquicanaliculate-type. *Prismatoolithus* and *Preprismatoolithus* eggs exhibit this morphotype.

Spheruprismatic - shell units are broad and the wedges of mammillae grade into prisms of the prismatic layer. The main distinctive character of this morphotype is that ratio of mammillary/prismatic layer, which is 1:1. The pore system is of the angusticanaliculate-type. This morphotype is exclusive of *Spheroprismatoolithus.*

Ornithoid - Ornithoid refers to fossil eggshells having a structure like that of modern ratite and neognathous birds. The tall and slender shell units consists of three to five ultrastructural zones including; basal plate groups, calcite radial ultrastructure (zone of radial calcite crystals), tabular ultrastructure (zone of wedges), squamatic ultrastructure (zone of squamatic aggregates), and external zone (zone of vertical crystals). Generally, shell units are fused with adjacent ones. Outer surface is mainly smooth but shows fine longitudinal grooves or ridges.

Neognathe - vertical boundaries of the shell units are relatively distinct and form an outer palisade layer that lies external and adjacent to the mammillary layer.

Ratite - vertical boundaries of shell units are non-distinct and form an outer continuous layer that lies external and adjacent to the mammillary layer.

SECTION 2

Systematic Paleontology and Phylogeny of fossil eggs

Chapter 4

RECORD AND CLASSIFICATION OF SAUROPOD EGGS

Fossil eggs attributed to sauropodomorph (Megaloolithidae, Faveoloolithidae and Similifaveoloolithidae) are one of the most common and diverse dinosaur egg-type in Mesozoic terrestrial ecosystems, and more specifically, during the Late Cretaceous (Carpenter and Alf, 1994; Carpenter, 1999). This fossil record covers a long time span, ranging from the Late Triassic to the end of the Cretaceous period; and showing a worldwide distribution, excepting Australia and Antarctica (Fig. 9) (Mikhailov, 1997; Carpenter, 1999).

4.1. SAUROPODOMORPH EGG RECORD: AN OVERVIEW ON ITS BIOGEOGRAPHICAL TIME DISTRIBUTION

Sauropodomorph includes largest land animals ever lived on Earth. According to current phylogeny of this group, two lineages can be distinguished: prosauropods and sauropods (Fig. 10). Prosauropods were medium-to-large-sized herbivorous dinosaurs (approx. 2.5 to 10 m length), facultative bipedal or quadrupedal with long necks and tails (Galton and Upchurch, 2004). In its turn, sauropods were gigantic quadrupedal herbivorous (4 to 35 m long) with long necks and tails, and robust limbs (Upchurch *et al.*, 2004).

These differences could also extend to their eggs (Fig. 10). Sauropod eggs are characteristic for their spherical shape (15 to 23 cm in diameter) with relatively thick eggshells, commonly up to 1.5 mm. Their shell units are well defined and delimited and a tubular gas-exchange canal system. Even so, some oospecies could show a complex system of pore canals (Vianey-Liaud *et al.*, 2003). On the other hand, eggs of prosauropods are smaller than previous ones, being 6-9 cm in diameter and ovoid in shape (Kitching, 1979; Reisz *et al.*, 2005). Unfortunately, no more information is taken from prosauropod eggshells, because all oological material attributed do this group of dinosaurs shows strong diagenetical process (Grine and Kitching, 1987; Zelenitsky

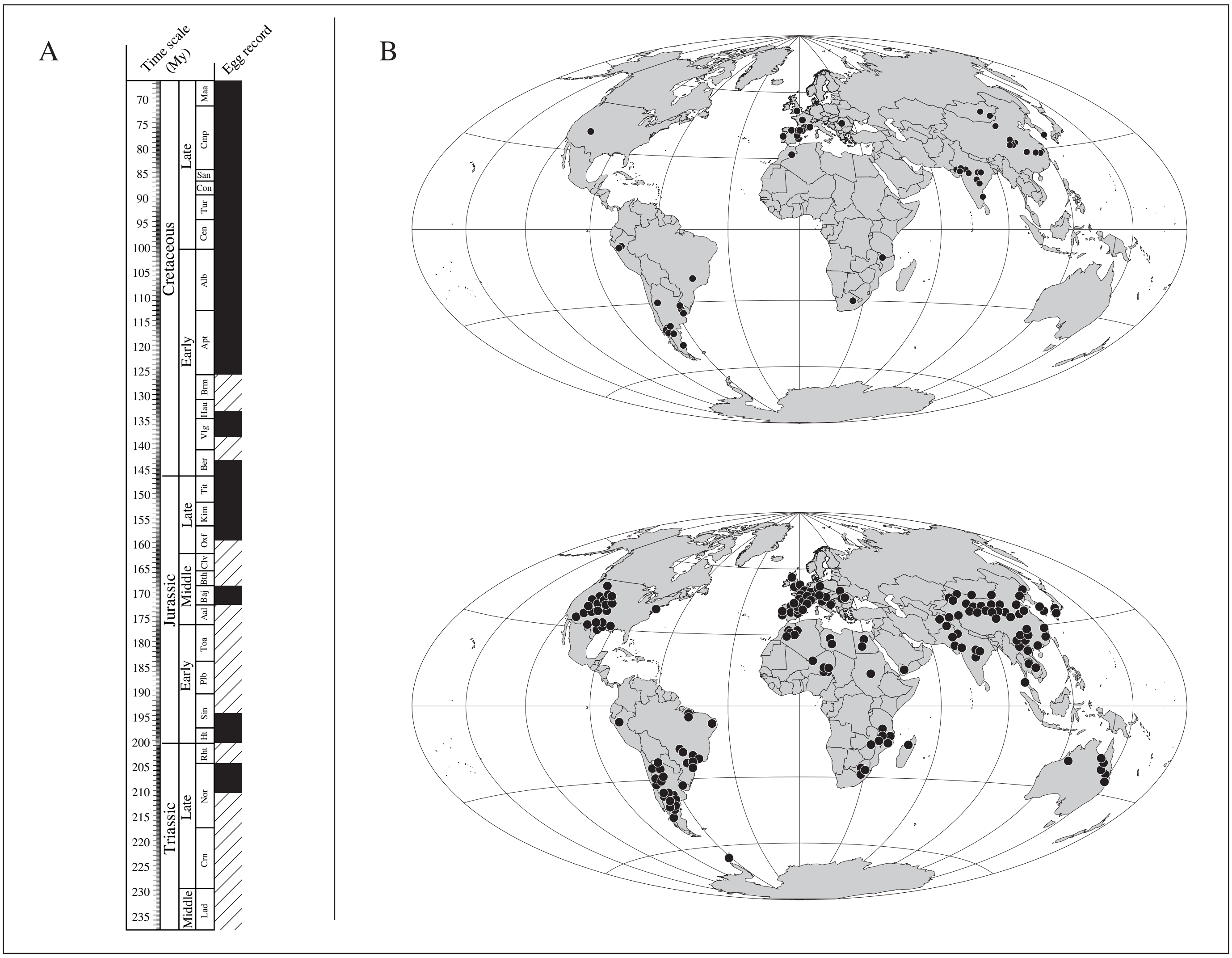

Figure 9. Distribution of oological remains attributed to sauropodomorphs. A) Temporal range of the oological record. B) Spatial distribution of oological record (upper) and other sauropodomorph remains (lower). Data source of the osteological record taken from Carpenter (1999) and Mannion and Upchurch (2010).

and Modesto, 2002).

Traditionally, two types of dinosaur parataxonomical families have been assigned to sauropod eggs: Megaloolithidae (Zhao 1979) and Faveoloolithidae (Zhao and Ding 1979); but recently a new oofamily, Similifaveoloolithidae (Wang *et al.*, 2011) has been proposed. The first oofamily is related to Macronaria sauropods base on embryological remains found within megaloolithid eggs from Patagonia (Argentina) (Chiappe *et al*, 1998), India (Wilson *et al.*, 2010), and Mongolia (Grellet-Tinner *et al.*, 2011). Nevertheless, this relationship was already supposed base on direct association of megaloolithid eggs and isolate titanosaur bones (Erben *et al.*, 1979; Vianey-Liaud *et al.*, 1987; Jain, 1994, Sahni *et al.*, 1994, among others). On the other hand, Faveoloolithidae eggs commonly appear associated to sauropod bones (Sochava, 1969; Faccio and Montaña, 1994; Mikhailov, 1997; Casadío *et al.*, 2002; Salgado *et al.*, 2007; Grellet-Tinner and Fiorelli, 2010), suggesting their possible relationship. But to date, not embryo has been found within this type of dinosaur eggs. Currently, Megaloolithidae includes 17 named and 5 unnamed oospecies, distributed from Europe, India, Africa, and South America and probably present in North America; while Faveoloolithidae is composed of 6 species of fossil eggs mainly presents in China, but also reported in Mongolia, South Chorea and South America. On the other hand, Similifaveoloolithidae is a monospecific oofamily reported only from China (Table 3).

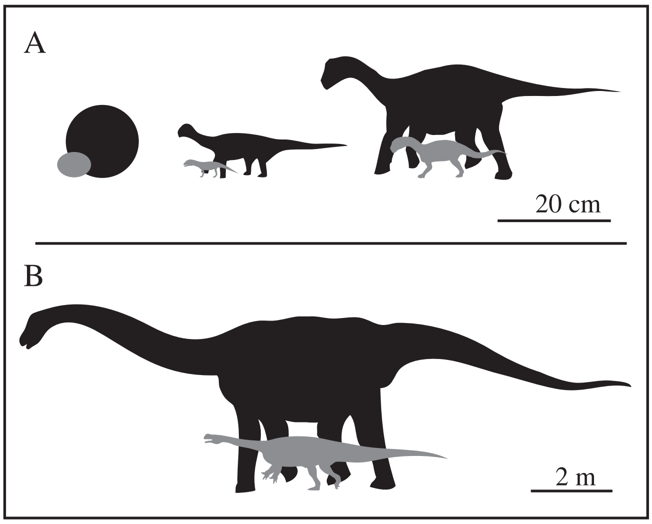

Figure 10. Size comparison between eggs and young (A) and adult (B) of prosauropod and sauropod.

During the last decades, the high amount of both megaloolithid and faveoloolithid eggs in Cretaceous deposits have motivated numerous studies on real parataxonomical diversity (Peitz, 2000a, b; Vianey-Liaud *et al.*, 2003; Panadès i Blas, 2002; Sander *et al.*, 2008; Zhang, 2010), structural and functional morphology (Grigorescu *et al.*, 1994; López-Martínez, 2000; Garcia and Vianey-Liaud, 2001a; Deeming, 2006; Jackson *et al.*, 2008; Grellet-Tinner and Fiorelli, 2010), their relationships between other fossil egg (Grellet-Tinner *et al.*, 2004; Garcia *et al.*, 2006; Moreno-Azanza *et al.*, 2008, Jin *et al.*, 2010), and their temporal distribution through the Cretaceous (Vianey-Liaud *et al.*, 1994; Vianey-Liaud and López-Martínez, 1997; Garcia, 1998; Garcia and Vianey-Liaud, 2001b; Vila *et al.*, 2011). But, until now, any study considers the whole sauropodomorph egg record.

The present chapter aims to reconstruct the biogeographical history of sauropodomorph eggs, establishing their spatial and temporal distribution during the Mesozoic, and their possible linkage with major events in sauropodomorph evolutionary history.

4.1.1. Sauropodomorph egg record

As it was mentioned previously, fossil egg record attributed to sauropodomorph show a long time span, and its record is reported in many continents (Fig. 9). However, this fossil record is not continuous and some gaps have been observed during the mesozoic; even most of the oological remains are represented by scattered eggshell fragments. Following, it is provided a list, temporally ordered, of sites where prosauropod or sauropod eggs have been discovered.

4.1.1.1. Triassic

Although the oldest sauropodomorph species is known from the Carnian (220 my) of Brazil (Langer *et al.*, 1999), it seems that this group of dinosaur could appear at the end of the Ladinian (Galton and Upchurch,

OOFAMILY	OOGENUS	OOSPECIES	TIME OCCURENCE	COUNTRY	Ref.
MEGALOOLITHIDAE	*MEGALOOLITHUS*	*aureliensis*	Late Campanian	Spain, France	Vianey-Liaud et al., 1994
		petralta	Late Campanian	Spain, France	Vianey-Liaud et al., 1994
		siruguei	Early Maastrichtian	Spain, France, Romania	Vianey-Liaud et al., 1994
		mamillare	Middle Maastrichtian	Spain, France, Romania	Vianey-Liaud et al., 1994
		microtuberculata	Late Campanian	France	Garcia & Vianey-Liaud 2001
		cylindricus	Late Maastrichtian	India	Khosla and Sahni, 1995
		mohabeyi	Late Maastrichtian	India	Khosla and Sahni, 1995
		padiyalensis	Late Maastrichtian	India	Khosla and Sahni, 1995
		jabalpurensis	Late Maastrichtian	India, Argentina	Khosla and Sahni, 1995
		dholiyaensis	Late Maastrichtian	India	Khosla and Sahni, 1995
		dhoridungriensis	Late Maastrichtian	India	Mohabey, 1998
		khempurensis	Late Maastrichtian	India	Mohabey, 1998
		megadermus	Late Maastrichtian	?France, India	Mohabey, 1998
		baghensis	Late Maastrichtian	Peru, France, Spain, India	Khosla and Sahni, 1995
		maghrebiensis	Late Maastrichtian	Morocco	Garcia et al., 2003
		Indet.	Bajocian	France	Garcia et al., 2006
		Indet.	Titonian	Portugal	Dantas et al., 1992
		Sp.1	Valenginian-Hauterivian	Spain	Moreno-Azanza et al., 2008
		Sp.2	Valenginian-Hauterivian	Spain	Moreno-Azanza et al., 2008
		Sp.	Early Maastrichtian	France	Garcia, 2000
		Sp.	Albian	Tanzania	Gottfried et al, 2004
	PSEUDOMEGALOOLITHUS	*atlasi*	Late Maastrichtian	Morocco	Garcia et al., 2003
	PATAGOOLITHUS	*salitraensis*	Late Campanian	Argentina	Simón, 2006

OOFAMILY	OOGENUS	OOSPECIES	TIME OCCURENCE	COUNTRY	Ref.
FAVEOLOOLITHIDAE	*YOUNGOOLITHUS*	*xianguaensis*	Albian	China	Zhao, 1979
		xipingensis	Santonian-Campanian	China	Fang et al., 1998
	FAVEOLOOLITHUS	*ningxiaensis*	Santonian-Campanian	China, Mongolia	Zhao and Ding, 1976
		zhangi	Albian	China	Jin, 2008
		= *Sphaerovum erbeni*	Campanian	Uruguay, Peru, Brazil, Argentina	Faccio & Montaña, 1994
	PARAFAVEOLOOLITHUS	*microporus*	Coniacian-Campanian	China	Zhang, 2010
		macropodus	Coniacian-Campanian	China	Zhang, 2010
		xipingensis	Coniacian-Campanian	China	Zhang, 2010
		tiansicunensis	Coniacian-Campanian	China	Zhang, 2010
		guoqingsiensis	Turonian	China	Wang et al., 2011
	HEMI*FAVEOLOOLITHIUS*	*muyushanensis*	Turonian	China	Wang et al., 2011
SIMILIFAVEOLOOLITHIDAE	*SIMILIFAVEOLOOLITHUS*	shuangtangensis	Turonian	China	Wang et al., 2011
Mussaurus eggs	unnamed	unnamed	Norian	Argentina	Bonaparte & Vince, 1979
Massospondylus eggs	unnamed	unnamed	Hettangian-Sinemurian	South Africa	Kitching, 1979

Table 3. List of oospecies attributed to sauropodomorph dinosaurs and ascribed to the oofamilies Megaloolithidae and Faveoloolithidae.

2004); coming more abundant during the Norian (230 my). The oldest site yielding prosauropod eggs is located in Santa Cruz Province (Argentina). In 1979, Bonaparte and Vince discovered seven post-hatchling dinosaurs near two small ovate eggs and some eggshells in the Norian part of El Tranquilo Group (Laguna Colorado Formation). The small skeletons (25-30 cm long) were interpreted as juveniles of South American prosauropod, *Mussaurus patagonicus* (Bonaparte and Vince, 1979; Pol and Powell, 2007). Unfortunately, any description or illustrations of those eggs were provided. Thus, nothing is known about the structure of eggs of first sauropodomorph dinosaurs.

4.1.1.2. Jurassic

At the beginning of the Jurassic, basal sauropods became the predominant herbivore fauna in all the major continental ecosystems. They were really abundant and diverse in South America, Africa and Eurasia, being also present in North America and Antarctica. Meanwhile, prosauropods suffered a dramatic decrease in their diversity, being completely extinguished at the end of the Early Jurassic (Galton and Upchurch, 2004). Only one site has provided oological material referred to sauropodomorph in the Early Jurassic. Located in the Hettangian-Sinemurian of the Upper Eliot Formation of South Africa (Kitching, 1979; Reisz *et al*., 2005), a partial clutch attributed to prosauropods containing six small ovoid eggs (5.5 - 6.5 cm in diameter) was found in reddish sandstone. Some of those eggs contained embryonic remain (Kitching, 1979). Years later, Reisz *et al*. (2005, 2010) confirmed that previous interpretation and they attributed the bone elements to nearly hatched prosauropod *Massospondylus carinatus*. Some eggshells were studied by Grine and Kitching (1987), concluding that the prosauropod eggshells exhibit similar structure those crocodilian. However, Zelenitsky and Modesto (2002) re-evaluated the same materials and suggested crocodilian characters were, indeed, an artefact of diagenetical process, which affect the real histostructure of the shell. Recently, Reisz *et al*. (2012) announced new oological discoveries in the same locality were the first clutch was found. They identified ten nests in four different horizons, suggesting nesting site fidelity. The most complete nest contains 34 subspherical eggs distribute in a single layer, and eggshells of those eggs are 0.1 mm of thick. But no information of shell microstructure is reported. Therefore, structure of prosauropod eggshell is still unknown.

During the Middle Jurassic, sauropods began to diversify and spread worldwide, while only three genera of prosauropods survived into this period (Galton and Upchurch, 2004; Upchurch *et al*., 2004). Only one site has provided sauropod oological material from this time. Garcia *et al*. (2006) reported the oldest megaloolithid eggshells from the Bajocian (aprox. 170 my) of Southwester France. They noted that those eggshells exhibit many structural characters also present in the Upper Cretaceous megaloolithid eggs from Europe, but Bajocian eggshells were, in average, ten time less thick that Cretaceous ones (0.2 mm *versus* 1-3 mm in thickness).

Sauropods have reached their zenith in diversity during the Late Jurassic (Upchurch and Barrett, 2005; Mannion and Upchurch, 2010). However, fossil eggs or eggshells attributed to this group are really rare and scarce for this time. Jensen (1970), Hirsch *et al.* (1989), Hirsch (1994b) and Bray and Hirsch (1998) reported some tubospherulithic eggshells from the Morrison Formation on Colorado (USA), which showed some similitude with eggshells found in the Upper Jurassic of Portugal (Dantas *et al*., 1991, 1992). These last remains from Portugal represent the youngest Jurassic eggs attributed to sauropod, which come from the Tithonian (Dantas *et al*., 1991, 1992). Dantas *et al.* (1992) pointed out the microstructure of Portuguese eggshells was, again, very similar to those Late Cretaceous megaloolithid eggs.

4.1.1.3. Cretaceous

If there is a period which could stand out for its richness on dinosaur egg, this is the Cretaceous. The quality, quantity and diversity of this fossil record cannot be compared with any other time in the Earth history. In general view, during this time, the oofamily Megaloolithidae is the most common group of fossil eggs attributed to sauropods but during the Cenomanian, and faveoloolithid eggs made their first apparition in Asia.

4.1.1.3.1. Early Cretaceous

At the beginning of the Cretaceous, the sauropod diversity remained more or less constant, with punctual increases and crisis (Mannion and Upchurch, 2010). At this time, this group was mainly represented by neosauropods, such as diplodocids (i.e. *Apatosaurus* and *Diplodocus*) and basal Macronaria (i.e. *Camarasaurus* and *Brachiosaurus*).

The oldest Cretaceous oological remains attributed to sauropods come from the Berriasian of South England. Ensom (1997, 2002) found some eggshells in the Purbeck Limestone Group. He tentatively assigned that eggshell fragments to Megaloolithidae oofamily, because they resembled of those Upper Cretaceous of France. More interestedly, Ensom (1997) attribute some few poorly preserved eggs to Faveoloolithidae oofamily, but they were not taking into consideration in their next works (see Ensom, 2002). For this reason, here we cannot consider those england shells as the first *Faveoloolithus*. Chronologically, next oological remains appear in the Valanginian-Hauterivian of El Castellar Fm. (Galve, Teruel Province, Spain) and the Villanueva de Huerva Fm. in (Zaragoza province, Spain). Initially, Kohring (1990a) and Amo-Sanjuan (1998) described the presence of some dinosauroid-spherulitic eggshell fragments from the Lower Cretaceous of Aragon. They did not refer that material to specific group of fossil egg, but Mikhailov (1997) suggested that those eggshells could belong to *Megaloolithus* oogenus. Later, Moreno-Azanza *et al*. (2008) recovered some thin eggshell fragments near the previous site yielding megaloolithis eggshells. Based on histrostructural characters exhibit by those eggshells, the authors attributed them to a megaloolithid type which show close phylogenetic relationship with Bajocian specimens from France (Garcia *et al*., 2006).

As a rule, African continent is very scarce in dinosaur fossil eggs, but it has provided one of the few remains of this record from the Mid-Cretaceous. In 1950, Swinton recovered two big rounded eggs (around 19 cm in diameter) near Mbeya city, in southwester Tanzania. Due to their poor preservation, Swinton (1950) could not report an accurate description of those materials. However, that author suggested that eggs could be related to sauropod dinosaurs based on its big size and their co-occurrence with sauropod bones in the same stratigrphical levels. More recently, Gottfried *et al*. (2004) reported some megaloolithid eggshells from the Unit I of the Red Sandstone Group, near Mbeya locality. That site, which is supposed coeval with the Cretaceous dinosaur beds of Malawi (?Aptian in age; Jacobs *et al*., 1990), seems to be the same where Swinton found the “sauropod eggs” fifty years ago. They observed that Tanzanian eggshells were very similar to some megaloolithid oospecies from the Late Cretaceous of France. However, the authors noted some differences in the porosity pattern between Tanzanian eggshells and those French, being higher in the African material than in the European one.

Although Central Asia is one of the richest areas with dinosaur fossil eggs, possible oological materials attributed to sauropod are rare (e.g. Kurzanov and Mikhailov, 1989). More recently, Grellet-Tinner *et al*., (2011) reported the oldest known lithostrotian titanosaur embryo *in ovo* from Algui Ulaan Tsav locality (Mongolia), which is Albian in age (Sukhanov, 2000). The specimen was found within a small rounded egg (8.7 x 9.1 cm in length); which is partially preserved as calcite geode. However, that egg shows similar thickness, ornamentation and microstructure than titanosaur eggs from Auca Mahuevo (Grellet-Tinner *et al*., 2004). Authors gave not any parataxonomical assignation to that egg, but according to information reported that specimen could be assigned to *Megaloolithus*.

South America is rich in dinosaur eggs from the Upper Cretaceous, but oological remains in the Lower Cretaceous are very unusual. Newly, Argañaraz (per. com., 2011) discovered a clutch of big rounded eggs (15 cm in diameter) in the Cerro Barcino Fm. from Chubut area (Patagonia, Argentina), which is Albian in age. According to information offered by Dr. Eloisa Argañaraz, those eggs doesn’t show the typical microstructure exhibited by *Megaloolithus* or *Faveoloolithus*, although they have been assigned to sauropod.

4.1.1.3.2. Late Cretaceous

For a long time, it was supposed that sauropods suffered a partial extinction during the mid-Cretaceous in North Hemisphere (Lucas and Hunt, 1989), being confined in southern continents and in Asia, and later they would have returned to the northern continents during the Campanian. However, this hypothesis was recently rejected (Mannion and Upchurch, 2010). During the Late Cretaceous titanosaurs were dominant sauropod group in the major terrestrial landmass.

ASIA

Asia is probably the richest place in the world with dinosaur eggs, being described more than 100 different oospecies, and some of these have been attributed to sauropod (Shochava, 1969; Young, 1979; Sabath, 1991; Mikhailov, 1991, 1994a; Mikhailov *et al*., 1994, among others). Sochava (1969, 1971, 1972) found a new type of dinosaur egg in the Gobi Desert of Mongolia, which showed an extremely thick eggshell (3-5 mm in thickness), and a complex network of gas-exchange canals (multicanaliculate pore system, *sensu* Mikhailov, 1997). Zhao and Ding (1976) found similar eggs in the Henan Province of China and proposed to erect the oofamily Faveoloolithidae. Initially, this oofamily includ two oogenus: *Faveoloolithius*, which is present in China, Mongolia and South Korea, and *Youngoolithus,* which is endemic from China. Later, Zhang (2010) erected the oogenus *Parafaveoloolithus*, which substitutes *Youngoolithus*. More recently, Wang *et al*. (2011) created a new oofamily, Similifaveoloolithidae, and erected the oogenus *Hemifaveoloolithus* (see Table 3).

Oldest remains of faveoloolithid eggs occur in the Cenomanian of China. They have been reported in the Gaogou Fm. of Xianguan Basin in Henan Province (Liang *et al*., 2009). Eggs and eggshells assigned to Faveoloolithidae are also present in the Turonian to Campanian of South Korea and China, and from the Santonian to Campanian of Mongolia (Table 4). Interestingly, until now, megaloolithid eggs are unreported from Asia.

SOUTH AMERICA

Eggs and eggshells attribute to sauropod are really abundant in the Upper Cretaceous continental deposits of South America, being present in Brazil, Uruguay, Peru and Argentina. These oological remains are represented by both Megaloolithidae and Faveoloolithidae oofamilies, but their distribution, abundance and diversity are different in each country.

Megaloolithidae is represented in South America for two oogenus: *Megaloolithus,* widely spreads in South

COUNTRY	PROVINCE	BASIN	OCCURRENCE
China	Hubei	Qiglong	Laijia Fm. (Coniacian to Campanian)
	Zhejiang	Jingu	Laijia Fm. Coniacian to Campanian
		Tiantai	Chichengshan Fm. (Turonian) Liangtouteng Fm. (Coniacian)
	Henan	Xixia	Sangping Fm. (Campanian to Maastrichtian)
		Xianguan	Gaogou Fm. (Cenomanian to Turonian)
		Wulichan	Majiacun Fm. (Coniacian to Santonian)
South Korea	Southern Jeolla	Boseong	Seonso Fm. (Late Cenomanian to Early Campanian)
		Whaseong	Shiwha Fm. (Turonian to Early Campanian)
Mongolian	Omnogov	Ologoy-Ulan-Tsav, Khermiyn-Tsav and Ikh-Shunkht	Barun Goyot Fm. (Santonian to Campanian)

Table 4. Faveoloolithidae record occurrences in Asia. (Data info from Sochava, 1969; Sabath, 1991; Mikhailov *et al*., 1994; Mikhailov, 1997; Shuvalov, 2000; Lee *et al*., 2000; Lee and Jeong, 2002; Huh and Zelenitsky, 2002; Lee, 2003; Kim *et al*., 2008; Liang *et al*., 2009).

America, and *Patagoolithus*, an endemic form of Central Argentina.

The oldest *Megaloolithus* from South America comes from Auca Mahuevo nesting site (Neuquén Province, Argentina), which is probably one of the best known and extensive egg-sites worldwide, providing thousands of eggs and clutches of sauropods (Chiappe *et al*., 2005 a, b). This site was discovered by Calvo *et al*. (1997), who reported some eggshell fragments near Neuquén city in the Lower Campanian Anacleto Fm. (Dingus *et al*., 2000). The authors proposed to erect a new oospecies (*Megaloolithus patagonicus*) with those eggshells, but Vianey-Liaud *et al*. (2003) suggested that *M. patagonicus* was a junior synonymy of *M. jabalpurensis* from India. Anyway, eggs and eggshells from Auca Mahuevo were doubtlessly attributable to *Megaloolithus* oogenus (Grellet-Tinner *et al*., 2004). The main importance of Auca Mahuevo nesting site rests on the fact that it was the first place where sauropod embryo were discovered, allowing to relate megaloolithid eggs and titanosaur sauropods (see, Chiappe *et al*., 1998, 2001; Salgado *et al*., 2005; García, 2007; Coria and Chiappe, 2007). This site has also provided information about nest structures of sauropods (Garrido *et al*., 2001; Chiappe *et al*., 2004) and some aspects of the reproductive biology of titanosaurs (see Jackson *et al*., 2003, 2004, 2008; Jackson, 2007).

Simón (2006) reported and describe the endemic oospecies *Patagoolithus salitralensis* from the lower part of the Allen Formation of Río Negro Province (Argentina) which is dated as Late Campanian-Early Maastrichtian in age (Novas, 2009; p.152, Fig. 4.8). She observed many similitudes between *P. salitralensis* and the oospecies of Auca Mahuevo, but eggshells from Río Negro Province differed from Neuquén ones in the eggshell thickness and in the coalescence of ornamental nodes, suggesting that each site had its own *Megaloolithus* oospecies. Salgado *et al*. (2007, 2009) reported the association of two types of megaloolithid eggs from many outcrops of Río Negro Province. They noted one of those types of eggs should be referred to *Patagoolithus* and the other shared many characters with *Megaloolithus* from Auca Mahuevo site. That observation implied that two types of megaloolithid eggs co-occurred in Central Argentina during the Early Cretaceous, and its turn they suggested the sharing of nesting site of two types of sauropods (Salgado *et al*., 2007, 2009). In fact, the Allen Fm. has the richest eggs record attributed to sauropods in Argentina. Dozens of faveoloolithid eggs have been reported from this geological formation in Río Negro and La Pampa Provinces (Uliana and Dellapé, 1982; Powell, 1985, 1987a, 1987b, 1992; Andreis, 1991; Bonaparte, 1991; Manera de Bianco, 1996, 2000; Magalhães Ribeiro, 1997; Simón, 1999, 2000, 2006; Manera de Bianco *et al*., 2000, Casadío *et al*., 2002, Salgado *et al*., 2007, Coria *et al*., 2010), but they are also present in Los Alamitos Fm. in Río Negro Province and the Los Llanos Fm. of La Rioja Province (Tauber, 2007; Grellet-Tinner and Fiorelli, 2010), both dated as Late Campanian-Early Maastrichtian in age.

Megaloolithus has been also recovered from Northwestern Peru. This material is present in the Maastrichtian of El Triunfo Fm. (Mourier *et al*., 1988; Vianey-Liaud *et al*., 1997), the Bagua Formation and the Upper Vilquechico Formation, which are Maastrichtian in age (Sigé, 1968; Kerourio and Sigé, 1984, Mourier *et al*., 1988; Carpenter and Alf, 1994). Those Peruvian eggshells were used by Vianey-Liaud *et al*. (1997) in the creation of *Megaloolithis pseudomamillare* oospecies. This oospecies is also present in the Marilia Formation of the Bauru Basin (southeastern Brazil), which is dated as Maastrichtian in age (Price, 1951; Magalhães Ribeiro, 1999, 2000, 2002; Grellet-Tinner and Zaher, 2007). Magalhães Ribeiro (2000) and Grellet-Tinner and Zaher (2007) emphasized the great similarity between that oospecies with those from France, Spain, India, Argentina and Peru.

Finally, the youngest “sauropod eggs” from South America, which have been assigned to *Faveoloolithus*, come from the Late Maastrichtian Mercedes Fm. and Gichón Fm. of Uruguay (Mones, 1980; Faccio, 1994; Faccio *et al*., 1990, Novas, 2009, Soto *et al*., 2012).

EUROPE

Megaloolithid eggshells, eggs and clutches are abundant in the Uppermost Cretaceous deposits of Europe. This type of dinosaur eggs has been found in Spain, France and Rumania.

In Spain, megaloolithid eggs and eggshells has been reported in fives provinces: Lleida, Barcelona, Burgos, Huesca and Valencia (Table 5, and see also Table 1). These remains are present in Campanian to Maastrichtian continental deposits and they are represented by several megaloolithid oospecies (see more details in Chapter 1) But the most well represented oospecies is *M. siruguei*, which is common for the Early Maastrichtian (Moratalla, 1993). The oldest Upper Cretaceous oological remains of Spain come from the South Pyrenees, from the Moror and Fontllonga-6 sites (Vianey-Liaud and López-Martínez, 1997; López-Martínez, 2000), which are dated as Late Campanian in age, while younger ones have been found in the Tremp Basin (Vianey-Liaud and López-Martínez, 1997). However, age of most of sites remains unclear or unknown, being difficult to evaluate their temporal situation. Even so, thank to new data provided in this theses and chronostratigraphical works made recently in Catalan fossiliferous sites (see Riera *et al*., 2009; Vila *et al*., 2011; and Chapter 8), it has been possible specify the position of some of these sites as well as the temporal succession of megaloolithid ootaxa.

PROVINCE/SITE		OOSPECIES	AGE	REFERENCES
Burgos	La Rosaca	*M. siruguei*	Maastrichtian	Alonso *et al*., 1991; Moratalla, 1993
	La Tejera	*M.siruguei*	Maastrichtian	Alonso *et al*., 1991; Bravo *et al*., 2006
	Quintanilla del Coco	*M.cf.mamillare*	Maastrichtian	Alonso *et al*., 1991; Moratalla, 1993
Cuenca	Portilla	*M.siruguei*	Late Campanian-Early Maastrichtian	Moratall, 1993 Ortega *et al*., 2008
Valencia	Bosna	*M. siruguei*	Maastrichtian	Moratalla, 1993; Company, 2008
	Collado Umán	*M. siruguei*	Maastrichtian	Moratalla, 1993; Company, 2008

Table 5. Non-Pyrenean egg-sites from Spain.

France contains an enormous amount of nest, eggs, and eggshells of *Megaloolithus*, which are mainly located in south and southeast of this country. Five different oospecies of *Megaloolithus* have been described in France, which range from the Late Campanian to Late Maastrichtian (Vianey-Liaud *et al*., 1994; Garcia, 1998; Garcia and Vianey-Liaud, 2001 a,b). They have been reported from different departments and in more than fifty sites (see Table 6). Paleoological works in France have been focused in parataxonomy (Vianey-Laiud and Crochet, 1993; Vianey-Liaud *et al*., 1994; Garcia, 2000; Garcia and Vianey-Liaud, 2001a; Cousin, 2002), biostratigraphy (Vianey-Laiud *et al*., 1994; Garcia and Vianey-Liaud, 2001b) and reproductive and nesting behaviors (Garcia, 1998; Cousin, 2002; Cojan *et al*., 2003).

All oological remains from Romania come from the continental Upper Cretaceous Dansuş-Ciula Fm. and Sânpetru Fm. (Grigorescu, 1994, 2006; Grigorescu and Ciski, 2008; Grigorescu *et al*., 1990, 2010). Only one megaloolithid oospecies has been identified, mainly by eggshell fragments because complete eggs are rare

Departament	Commune	Site	References
Aude	Corbières	Albas, Fontfroide	Lapparent, 1967; Plaziat, 1961; Erben *et al*., 1979; Penner, 1985; Cousin, 1997b, 2002; Cousin and Breton, 2000
	Narbonn	Argeliers	Lapparent, 1967; Vianey-Liaud *et al*., 1994
	St. André-de - Roquelongue		Lapparent, 1967; Cousin, 2002
	Rennes-le-Château		Breton *et al*., 1986; Cousin, 1995, 1997a, 2002; Cousin *et al*., 1989, 1994
Ariège	Le Mas-d' Azil		Le Loeuff, 1991
Bouches-du-Rhône	Beaurecueil	Les Roques-Hautes, Les Grands-Creux, Crete-du-Marbre	Lapparent, 1947; Dughi and Sirugué, 1976, Penner, 1985
	Meyreuil	Le Pujet	Vianey-Liaud, 2011 per. com.
	Tholonet	Pont- Canal de Doudon	Vianey-Liaud, 2011 per. com.
	Rousset-sur-Arc	St. Privat, Le Ribas, La Cairanne La Colline de Chapeliers, Frigara, La Bégude	Lapparent, 1967; Penner , 1983 , 1985; Williams *et al*., 1984 ; Cousin *et al*., 1987; Vianey-Liaud *et al*., 1994; Garcia, 1998
	Châteauneuf-le-Rouge	St. Jean-de-Melissanne, Echangeur de la Barque	Vianey-Liaud, 2011 per. com.
	Puyloubier	Angelin, La Grande Pugere, St.-Ser 1 and 2, Bramefan, Piconin, Patiras 1 and 2, L'Avocat, Station de Pompage, St. Pons, Genty	Dughi and Sirugue , 1958; Kérourio, 1981; Vianey-Liaud, 2011 per. com.
	Trets	La Bastidonne 1 and 2, St. Catherine, Malbarrate, Courtot, La Neuve	Vianey-Liaud, 2011 per. com.
	St. Mitre-les-Remparts	Figuerolles, La Caudiere, Caderaou 1 and 2, L'Etang de Berre	Vianey-Liaud, 2011 per. com.
	Velaux		Cousin et al., 1997
	Maussane-les-Alpilles	Maussane	Lapparent, 1967
	Eygalières		Lapparent, 1967
	Les Pennes-Mirabeau	Sextius	Buffeteaut, 2000; Cousin, 2002
	Rognac		Lapparent, 1967
	Champ-Garimond		Sigué *et al.*, 1997
Hérault	Chateau Castigno		Lapparent, 1967
	Lunas		Cousin, 2002
	Mèze		Garcia, 1998
	Montpellier	Montpellier	Lapparent, 1967
	Pierrerue		Marcou, 1994
	St. Chinian		Lapparent, 1967
	Villeveyrac		Lapparent, 1967
Var	Cotignac	Château-de-Rognette	Lapparent, 1967
	Fox-Amphoux		Lapparent, 1967
	Montmeyan		Lapparent, 1967
	Pourrières-Pourceiux	Arc de Triomphe de Marius	Lapparent, 1967; Williams et al., 1984; Vianey-Liaud, 2011 per. com.
	Rians		Lapparent, 1967
	Salernes		Lapparent, 1967

Table 6. Dinosaur egg-sites yielding megaloolithid eggs in Southwestern France.

in the Rumanian sites (Grigorescu, 1994). But more interesting is that this megaloolithid oospecies has been associated to hadrosaur hatchling remains (Grigorescu 2003, 2006; Grigorescu *et al*., 2010), suggesting that hadrosaurs also could laid megaloolithid eggs. If this interpretation is correct, it would means that different dinosaurs could laid a same type of egg.

INDIA

The Indian subcontinent has yield thousands of dinosaur nests, eggs and eggshells assigned to *Megaloolithus*, which have been largely documented in the literature (see Mohabey, 1984, 1991, 1996, 1998; Jain and Sahni, 1985; Srivastava *et al*., 1986; Vianey-Liaud *et al*., 1987, 2003; Mohabey and Mathur, 1989; Sahni, 1993; Bajpai *et al*., 1993; Sahni *et al*., 1994, Khosla and Sahni, 1995; Kohring *et al*., 1996, among others). All of them have been recovered from the Uppermost Cretaceous beds of the Lameta Formation and Intertrapped beds of Deccan volcano-sedimentary sequence, which are dated to Maastrichtian in age. There is a great controversy about the oological diversity of the Indian megaloolithid eggs. Initially, Khosla and Sahni (1995) described seven oospecies of *Megaloolithus*, coming from many site of Madhya Pradesh state, in the central region of India. Few years later, Mohabey (1996, 1998) identified eight new types of *Megaloolithus* from Maharashtra and Gujarat states, in the western coast of India. Trying to put order in this topic, Vianey-Liaud *et al*. (2003) revised all the oological material described previously and it was compared with well known European megaloolithid oospecies. Finally, they accepted only nine Indian oospecies as valid taxa, while the rest were considered junior synonymous from other ones. They also revealed the high similitude between European, South American and Indian megaloolithid eggs.

Indian sites have corroborated the relationship between megaloolithid eggs and titanosaur sauropods. Wilson *et al*. (2010) found a partial clutch of *Megaloolithud dhoridungriensis* near Dholi Dungri village in Gujarat, western India. One of those eggs contained embryological remains, which have been described as belonging to titanosaur hatchling. This new evidence reinforces the idea that titanosaurs sauropods laid megaloolithid eggs.

AFRICA

The Maastrichtian richest egg-site in North Africa is located in the north-eastern part of Morocco, where at least five oospecies have been described from the upper part of Irbzer Formation (Garcia *et al*., 2003; Vianey-Liaud and Garcia., 2003). Eggshells attributed to sauropod, belonging to the oofamily Megaloolithidae, are represented by *Megaloolithus maghrebiensis* (Garcia *et al*., 2003) and *Pseudomegaloolithus atlasi* (Vianey-

Liaud and Garcia, 2003) in this site. Few eggshells have been recovered from Achlouj-2 site, but they are enough to confirm the presence of megaloolithid eggs in the Late Cretaceous of North Africa. Garcia *et al.* (2003) and Vianey-Liaud and Garcia (2003) stressed the great similarity between African eggshells and some European oospecies, as *Megaloolithus siruguei* and *Megaloolithus baghensis*.

4.1.2. Fossil egg record and paleogeographical history of sauropodomorph dinosaurs.

As it is shown above, oological record attributed to sauropodomorph dinosaurs range from the Norian (Late Triassic) to the end of the Maastrichtian (Late Cretaceous) and its presence in major continents, excluding Antarctica and Australia. Unfortunately, this record is not continuous in each landmass, being important gaps of time without oological record. These gaps could be consequence of the real absence of the record, taphonomical processes or sampling bias. Considering that sauropodomorph dinosaurs were present during all Mesozoic (Mannion and Upchurch, 2010), the oological record associated to them must be present for the same time, too. Maybe, this gap of record could be motivated by the absence of favorable sedimentary facies where to find oological material. In other words, fossil eggs tend to be located in continental deposits, mainly in fluvial and alluvial facies (Riera, 2010); but along Earth history the presence or the abundance of these environments have changed, causing many type of bias in fossil record (Mannion and Upchurch, 2010). Furthermore, it is obvious that the study and the sampling of fossil eggs is a relatively young discipline in paleontology and few persons have dedicated enough time to collect these type of fossils. Apparently, there are no reasons to think about absolute absence of fossil egg record.

Here, we just want to note that if oological record is taken together, it is possible to establish some links whit some major events in the history of sauropodomorph dinosaurs. But this task is only possible if we assume a particular condition: although the mineral structure of the eggshell is relatively strong, it cannot be largely transported or removed. Experiments in modern gull eggs reveal that eggshells are easily broken under wind or water flow conditions (Hayward *et al.*, 2000, 2011). Therefore, the finding of large eggshells fragments might indicate the proximity of a nesting zone, assuming the *in situ* character of the remains both in time as in space. Thus, the presence of oological remains could also indicate the presence of its producer.

Despite the speculative component of the following work it could be establish the basis of future studies.

4.1.2.1. The origin of Sauropodomorph (Late Triassic to Early Jurassic)

The exact place and time of the appearance of sauropodomorph dinosaurs is still unknown. The earliest prosauropods known are *Saturnalia tupiniquim* (Langer *et al*., 1997) and *Panphagia protos* (Martínez and Alcober, 2009), which have been found in the Early Carnian of Brazil and Argentina, respectively. Oldest oological remains from The Norian of Argentina (Bonaparte and Vince, 1979) are confident with the temporal and spatial distribution of those first sauropodomorph dinosaurs. Since their first appearances, prosauropods diversified and distributed quickly during the Late Triassic and the Early Jurassic, first from Gondwana and then migrating to Laurasia (Upchurch, 1995; Galton and Upchurch, 2004). The presence of nest attributed to *Massospondylus* in the Hettangian-Sinemurian of South Africa (Kitching, 1979; Reisz *et al*., 2005) could reflect that dispersal pattern (Fig. 11A).

4.1.2.2. Rise of sauropods and the domain of Neosauropoda (Middle Jurassic to Late Jurassic)

At the end of the Early Jurassic, prosauropods become extinct and sauropods rose as dominant herbivorous in Mesozoic continental ecosystems (Upchurch, 1995). At the same time, Asian plate separated from others Laurasian landmass becoming isolated for a long time. This isolation produced an endemic dinosaur fauna, where sauropods were represented by *Euhelopoidae* family, which includes the huge forms *Mamenchisaurus* and *Omeiasaurus*. For its part, at the beginning of the Middle Jurassic a new group of advanced sauropods, called Neosauropoda, appears all over the world (Upchurch, 1995). This group was geographically widespread tanks to the connection between Gondwana and Laurasia. After, at the end of the Middle Jurassic, both supercontinents were separated and that separation produced a differentiation within neosauropod faunas of North and South. For example, diplodocids and camarasaurids were dominant in North America and Europe, while dicraeosaurids were abundant in Africa and South America (Upchurch, 1995). However, there are difficulties with this simple picture of neosauropod biogeography, and in particular with the presence of brachiosaurids in both North America and Africa during the Late Jurassic. If Laurasia and Gondwana were completely separated during the Callovian, they must be connected sometime during Late Jurassic. It has been proposed a possible scenario where these two continents could be connected for a “land bridge”, which could be Western Europe (Russell, 1993; Sereno *et al*, 1994; Upchurch, 1995).

The lack of prosauropod eggs in the oological record seems consistent with the idea of the absence of this group of dinosaurs during the Mid-Late Jurassic. On its turn, oological material attributed to sauropods is really scarce in this period of time. Oldest megaloolithid eggshells date from the Bajocian of France (Garcia *et al*., 2006), being also present in the Kimmeridgian of North America (Bray and Hirch, 1998) and in the Tithonian of Portugal (Dantas *et al*., 1992). At first glance, the Laurasian distribution of this record apparently is not linked with a specific event of neosauropod biogeography distribution. Interestingly, these oological remains are frequently associated to Laurasian neosauropods, such as camarasaurids, brachiosaurids and diplodocids. Garcia *et al.* (2006) suggested that the Laurasian neosauropods could be the potential parental candidates for the Bajocian *Megaloolithus*. Assuming that, megaloolithid Jurassic eggs could be laid for some taxon phylogeneticaly related with titanosaur sauropods, like brachiosaurids (Garcia *et al.*, 2006), but this group of dinosaurs did not appear until the Late Jurassic (Upchurch, 1995; Galton and Upchurch, 2004), being more probable a relationship with camarasaurids. In fact, this link between early megaloolithid eggs and camarasaurids could be also inferred with the North American oological record. Megaloolithid eggshells reported by Bray and Hirsch (1998) were found near the locality where Britt and Naylor (1994) discovered embryonic bones of *Camarasaurus* sp.; both records coming from equivalent levels of the Morrison Fm. Similar relations could be established with the Tithonian megaloolithid eggs of Lourinhã (Dantas *et al.*, 1992), which were found near the site where was found the camarasurid *Lourinhasaurus* Dantas *et al.* (1998).

Although no direct evidence which could confirm this relationship (e.g. embryo *in ovo*), it cannot be assured the relationship between Jurassic oological remains and camarasaurid sauropods. However, all evidences point to a possible relationship with Laurasian neosauropods (Fig. 11B).

4.1.2.3. European "land bridge": the dispersion of Macronaria sauropods and the rise of titanosaurs (Early Cretaceous)

Gondwana and Laurasia were separated for a long time in the Jurassic, but a probable connection could occur between North America and Africa, via Europe, during the Late Jurassic and the Early Cretaceous, allowing the migration of sauropod fauna between continents. At the end of the Jurassic, sauropod faunas from North and South hemispheres were substantially different. In Europe and North America, sauropods were manly represented by diplodocids, camarasaurids and brachiosaurids, while dicraeosaurids and titanosaurids dominated South America and Africa (Upchurch, 1995). The oldest record of titanosaurs appeared in the Kimmeridgian of Tanzania. This group of sauropods was relatively abundant in the Late Jurassic but becomes the dominant fauna during the Early Cretaceous, even being present in northern continents.

Most oological material attributed to sauropod from the Early Cretaceous has been found in the Iberian Peninsula, but it is also reported from South England (Ensom, 2002). This type of eggs is scarce and rear if it is compared with other groups of fossil eggs from the same time, such as *Elongatoolithus* or *Macroolithus* both attributed to theropod dinosaurs (Amo-Sanjuan, 1998).

As was mentioned, during the Late Jurassic and Early Cretaceous some sauropod groups migrated from the North to the South Hemispheres, or vice versa, tanks to the connection between regions, via the southwestern part of Europe (Portugal and Iberian Peninsula). Therefore, it is not surprising that Iberian Peninsula records a great diversity of sauropods, such as diplodocids (e.g. *Dinheirosaurus* Bonaparte and Mateus, 1999 and *Demandasaurus* Fernández-Baldor *et al.*, 2011), brachiosaurids (*Lusotitan* Antunes and Mateus, 2003), camarasaurids (*Aragosaurus* Sanz *et al.*, 1987 and *Tastavinsaurus* Canudo *et al.*, 2008), cetiosaurids (*Lourinhasaurus* Dantas *et al.*, 1998), and even endemic turiasaurids (*Galvesaurus* Barco *et al.,* 2005, *Losillasaurus* Casanovas *et al.*, 2001 and *Turiasaurus* Royo-Torres *et al.*, 2006). This diversity in sauropod fauna could be explained because Iberian Peninsula served as a crossroad for the dispersion of many sauropod groups. Thus, it is not rare that most of sauropod eggs reported from that period of time were found in this region. So far, we cannot find any satisfactory explanation for the lag of oological record in southern continents, North America or Asia, but it could be related with sampling bias or by the absence of appropriate facies for the preservation of these remain (Fig. 11C)

4.1.2.4. Sauropod "Mid-Cretaceous hiatus" in northern continents and new ootaxa (Middle Cretaceous: from Aptian to Santonian)

The mid-Cretaceous of North America and Europe is characterized for the absence of sauropod fossils. This evidence led to several authors to suggest a possible sauropod extinction. But a recent re-evaluation on this topic demonstrated the most plausibly interpretation for the absence of sauropod record could be produced by sampling bias, to the rarity of inland sediments and to the dominance of coastal deposits preserved in northern continents during the mid-Cretaceous (Mannion and Upchurch, 2010). Meanwhile, Gondwana sauropod faunas were dominated by titanosaurs, which dispersed from Africa to South America, India and Australia before the Aptian (Upchurch, 1995). In its turn, sauropod faunas from Asian continent were composed mainly by titanosauriforms sauropods and basal titanosaurs, which had entered in Asian continent during the Jurassic (Upchurch, 1995).

Two scenarios related with the oological record will be considered below. One concerns the absence of fossil record in north continents and the other tears about the apparition of faveoloolithid eggs in Asia.

Most fossil eggs referred to sauropod have been attributed to Megaloolithidae oofamily, which has been reported mainly in Gondwana continents (Africa and South America) but also in Mongolia. This peculiar distribution of the sauropod oological record and its absence in Laurasian continents could be related with the same factors suggested for the "Mid-Cretaceous sauropod hiatus". In one hand, decrease of inland facies during the Middle Cretaceous could have conditioned the presence or absence of favorable potential nesting zones in the North Hemisphere. It is well known sauropods laid their eggs in continental facies, mainly in fluvial system (Bhattacharya and Mohabey, 1991; Cojan *et al.*, 2003; Chiappe *et al.*, 2005a, b; Therrien *et* *al*, 2009; Riera, 2010, among others). A reduction of these areas could force to these animals to do their egg-laying in other environments lees suitable for fossilization of eggs. That decrease in continental sediments did not occurred in South America, Africa or Asia (Mannion and Upchurch, 2010), allowing titanosaurs to make their egg-laying in a potential fossiliferous environment.

First faveoloolithid eggs appear in the Cenomanian of China, and this group is widely distributed from Asia till the end of the Cretaceous. As was mentioned previously, *Faveoloolithus* has been related to sauropods in base to the co-occurrence of both oological and skeletal record in same stratigraphyc levels. But it is hard to understand why it appears during the Middle Cretaceous and their relation with Asian sauropod, because sauropod fauna of this continent is not well known and this difficult to establish relationships between this new ootaxa and sauropod groups. However, it seems reasonable to suggest an endemic origin for *Faveoloolithus*, in other words, the endemic character of the new ootaxa could imply endemic Asiatic egg-laying sauropods, such as nemegtosaurids (Fig. 11D)

4.1.2.5. Austral immigration of titanosaurs (Late Cretaceous: from Campanian to Maastrichtian)

At the end of the Cretaceous, titanosaurs were the dominant sauropod fauna worldwide, being represented by tens of genus (Upchurch *et al*., 2004). The most important event in the biogeographycal history of this group during the Late Cretaceous is the probable invasion of titanosaurs from southern continents to northern ones. Apparently, *Alamosaurus* from New Mexico could come from the immigration of South America titanosaurs, and endemic dwarf titanosaurs from Europe could be related with African sauropod immigrates (Upchurch, 1995). In this time, Madagascar and India were isolated and Asia was separated in its eastern margin from Europe by shallow epicontinental seas.

Unfortunately, it is no possible infer that the migration event is based in the oological record. Sauropod eggs from the Late Cretaceous show a Gondwanian distribution, being present in South America, North Africa and India but also in Europe (Fig. 11D). Only if southern egg-sites were older than northern one, it could reflect a possible latitudinal dispersion thought time. But no differences in age distribution occur between northern and southern egg-sites; even some southern egg-sites seem to be younger than northern (Fig. 12). A probable explanation for this difference between both paleogeographical history of sauropods and their fossil egg record could be explained in terms of taphonomical bias or by the presence/absence of favorable sedimentary facies where to find these oological materials, as could occur with Mid-Cretaceous oological record.

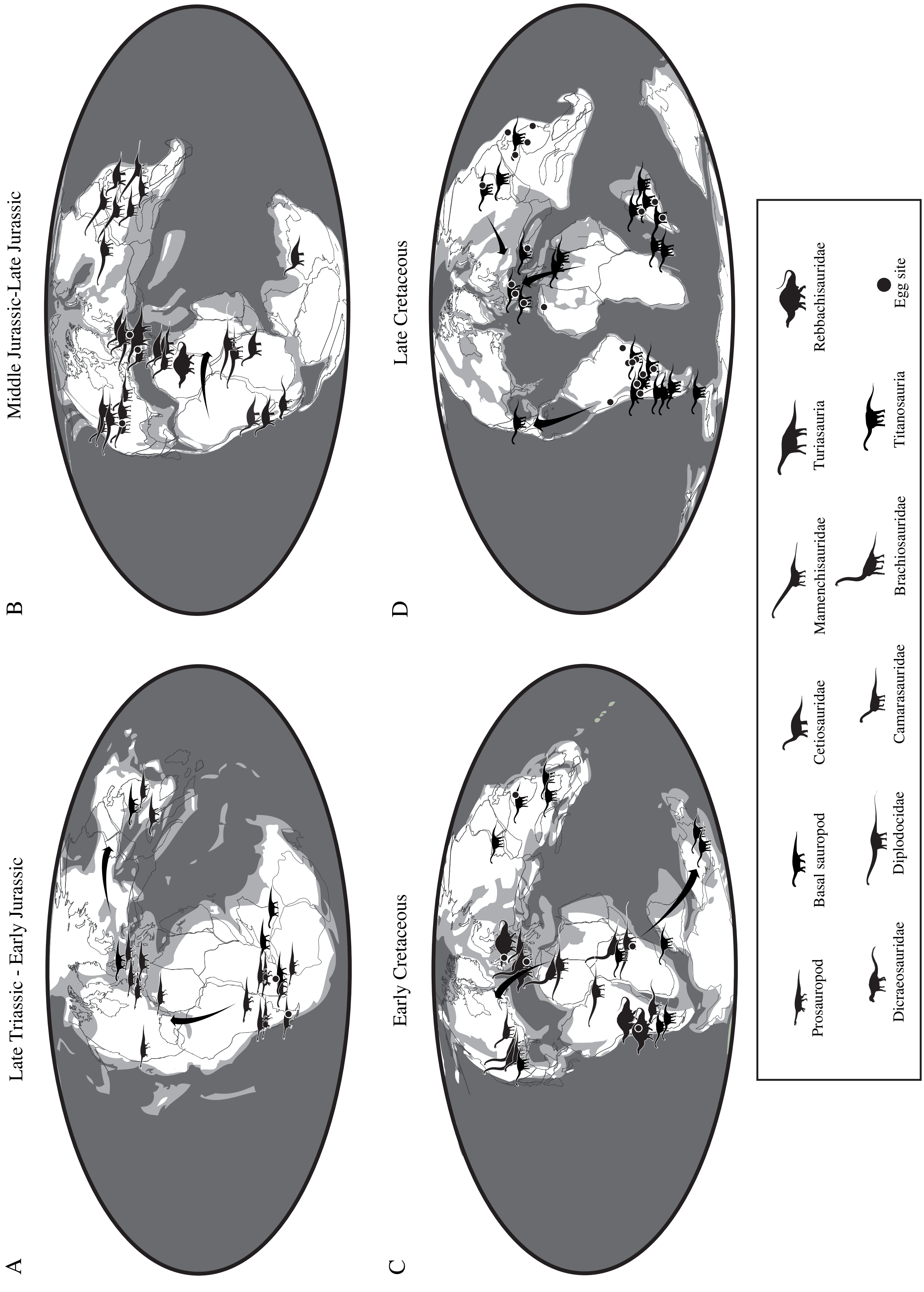

Figure 11. Biogeographical distribution of sauropodomorphs and its relation with its oological record during Mesozoic Era. (A) The Late Triassic - Early Jurassic. (B) The Middle - Late Jurassic. (C) The Early Cretaceous. (D) The Late Cretaceous. Black arrows indicate the main dispersal events.

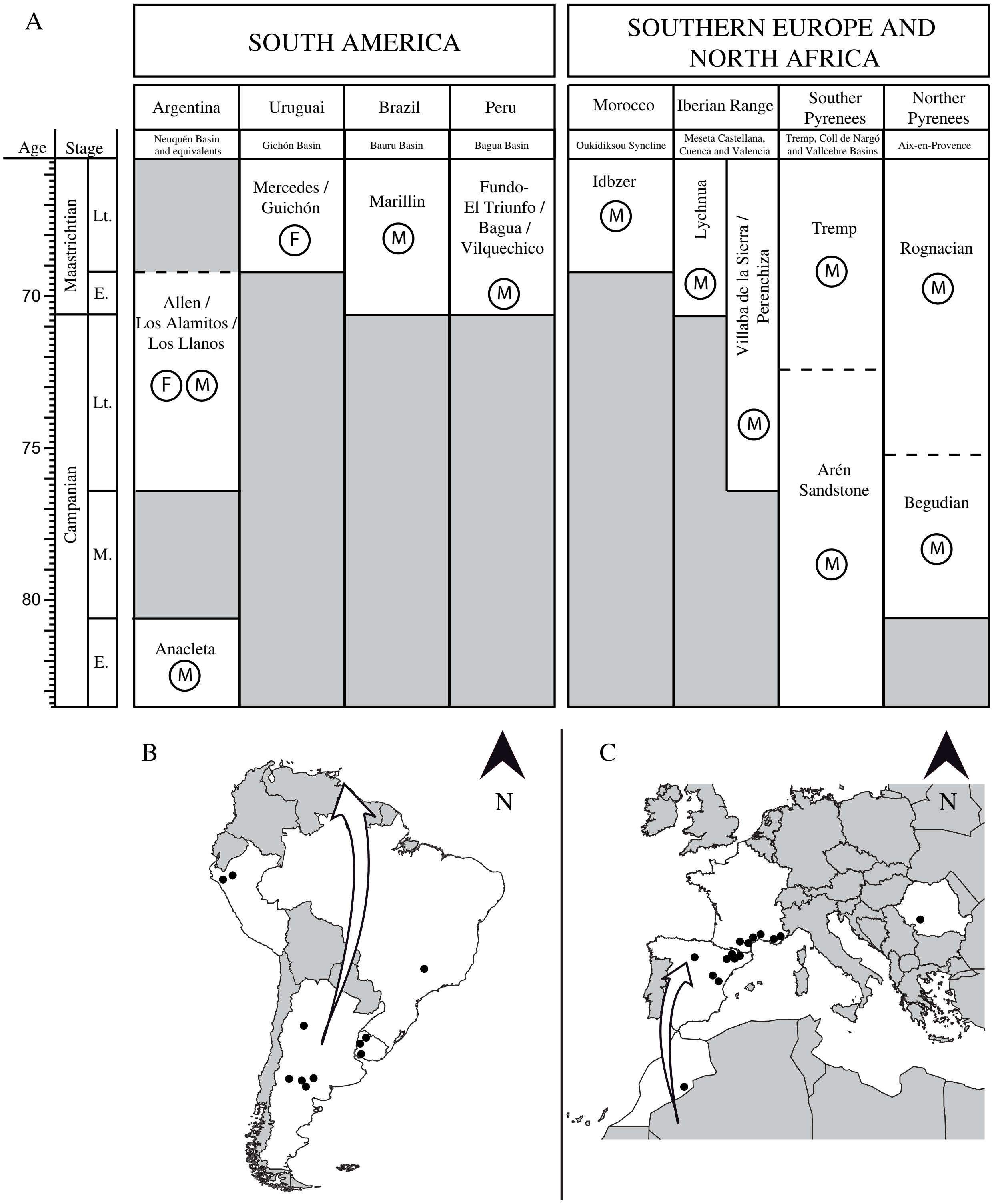

Figure 12. (A) Stratigraphy of sauropod egg-bearing Upper Cretaceous formaions of South America and Europe. Map of South America (B) and North Africa-Europe (C) indicating fossil localities that have yield Upper Cretaceous sauropod's eggs. White arrow shows the possible direction of southern immigration event. F - Faveoloolithus, M - Megaloolithus.

4.2. PROBLEMATICS IN MEGALOOLITHID EGGS: DIAGNOSTIC CRITERIA AND VALIDITY OF OOSPECIES

As it could be seen in the previous chapter, sauropod eggs are wide-world distributed and rang a long time span, being one of the most common and abundant dinosaur egg-type even know (Carpenter, 1999). At the end of twentieth century, there were 24 described oospecies associated to Megaloolithidae oofamily, which were included in two oogenus: *Megaloolithus* and *Cairanoolithus* (but see Chap. 4.2.1).

In addition, the highest part of *Megaloolithus* oospecies was concentrated in a relative short interval of geological time, ranging from the Late Campanian to the Late Maastrichtian (less than 7 millions of years). Furthermore, that high oological diversity did not match whit sauropod record of the same period, being more oospecies than dinosaurs (Panades i Blas, 2002). This situation led to some paleontologists doubted about the validity of some previously purposed oospecies and the usefully of the parataxonomy. For example, some German paleontologists, who worked for a long time in Catalan egg-sites, proposed to refer all the megaloolithus ootaxa to only one oospecies, based on the lack of useful microstructural criteria (Peitz, 2000a, b; Sander *et al*., 2008). Another point of view was established by Grellet-Tinner *et al*. (2004). They studied tens of megaloolithid eggs from the Argentinean Auca Mahuevo site, observing the high variability and diversity of shape in those eggs, even from the same nest. Thus, they argued that without large amount of samples it would be better not create new ootaxon, because something that initially could seems a new oospecies could be, indeed, the result of intraspecific variations or consequence of taphonomical and diagenetical process. Following this way, Salgado *et al*. (2007) avoid to use the parataxonomical classification. They provide accurate descriptions of oological remains but without put a parataxonomical name to those remains.

In 2003, Vianey-Liaud and colleges made a review about megaloolithid oospecies from Europe, India and South America. They proposed the synonymy of several *Megaloolithus* oospecies, based on the great micro- and macrostructural similitude between some ootaxa from India and Europe, keeping valid 17 of the 24 initial ootaxa (Table 7).

Apparently, the work of Vianey-Liaud *et al*. (2003) marked a point of inflection in the increasing trend of creation of new *Megaloolithus* oospecies. However, and more recently, three new oospecies and two new oogenus have been attached to this group of fossil eggs (see Vianey-Liaud and Garcia, 2004; Garcia *et al*., 2004; Simón, 2006).

Therefore, nowadays the parataxonomical family Megaloolithidae includes four oogenus: *Megaloolithus, Patagoolithus, Pseudomegaloolithus* and *Cairanoolithus*; and 20 oospecies. Considering the eggshell as a very conservative structure, this number of megaloolithid oospecies is still very high for a period of 6.5 My.

OOFAM.	OOGEN.	OOSPECIE	TIME OCCURENCE	COUNTRY	Ref.
MEGALOOLITHIDAE	*MEGALOOLITHUS*	*aureliensis*	Late Campanian	Spain, France	Vianey-Liaud *et al.*, 1994
		petralta	Late Campanian	Spain, France	Vianey-Liaud *et al.*, 1994
		siruguei	Early Maastrichtian	Spain, France, Romania	Vianey-Liaud *et al.*, 1994
		mamillare	Late Maastrichtian	Spain, France, Romania	Vianey-Liaud *et al.*, 1994
		microtuberculata	Late Campanian	France	Garcia and Vianey-Liaud, 2001a
		cylindricus	Late Maastrichtian	India	Khosla and Sahni, 1995
		mohabeyi	Late Maastrichtian	India	Khosla and Sahni, 1995
		padiyalensis	Late Maastrichtian	India	Khosla and Sahni, 1995
		jabalpurensis	Late Maastrichtian	India, Argentina	Khosla and Sahni, 1995
		dholiyaensis	Late Maastrichtian	India	Khosla and Sahni, 1995
		dhoridungriensis	Late Maastrichtian	India	Mohabey, 1998
		khempurensis	Late Maastrichtian	India	Mohabey, 1998
		megadermus	Late Maastrichtian	?France, India	Mohabey, 1998
		baghensis	Late Maastrichtian	India	Khosla and Sahni, 1995
		problematica	Late Maastrichtian	India	Mohabey, 1998
		maghrebiensis	Late Maastrichtian	Morocco	Garcia *et al.*, 2003
	? CAIRANOOLITHUS	*roussetensis*	Late Campanian	France	Vianey-Liaud *et al.*, 1994
		doughii	Late Campanian	France	Vianey-Liaud *et al.*, 1994
	PSEUDOMEGALOOLITHUS	*atlasi*	Late Maastrichtian	Morocco	Garcia *et al.*, 2003
	PATAGOOLITHUS	*salitraensis*	Late Campanian	Argentina	Simón, 2006

Table 7. List of oospecies included in the Megaloolithidae oofamily.

In this chapter, it will be discussed the validity of structural features used in the characterization of megaloolithid ootaxa and it will be reevaluate the validity of current megaloolithid oospecies.

4.2.1. Structural levels and characters

Not all microstructural features observables in an egg can be included in morphotype description (see Chapter 3.2). For example, some characters related with prismatic and external zones only can be used in avian or theropod dinosaur eggs (see Mikhailov, 1991, 1997). Other characters seem to be restricted to one specific morphotype, such as the presence of acicular crystals of aragonite, which are only present in turtle eggshells, or the basal plate group which is exclusive for crocodile eggshells. Thus, megaloolithid eggs can only exhibit structural characters typically of spherulithic morphotype. Following, it is listed the classical macro- and micostructural features used in the description of megaloolithid eggs, and it is discussed their validity for each one:

Egg shape and size: Extant reptilian eggs exhibit extraordinary variation in size and shape, which range from nearly spherical to over 15 times as long as wide (Iverson and Ewert, 1991). Unlike birds, "reptilian" egg (lizard, snakes, turtles and crocodiles) shows a symmetrical bicone in shape, while avian egg is clearly asymmetrical. Many factors control the final size and shape of reptilian eggs. Some of these factors are directly related whit physiological aspects of female, such as its size, age and experience, its oviduct/ abdominal space and morphology or even the order of ovoposition of eggs. But other factors are more related with environmental factors, such as the resource constrictions, climatic conditions or time of seasons, which could affect the final size or shape of egg (Iverson and Ewert, 1991). The combination of these factors condition the intra-specific variation of eggs from the same species, which , in extant amniotes, could represent more than 10% of the intra-specific variation (see Takahashi and Iwasawa, 1990; Petersen, 1992; Williams, 1994; Piña *et al*., 1996; Profu *et al*., 2004; Rafferty *et al*., 2005; among others).

However, this character is more difficult to obtain with confidence. It is possible to measure the size of a single egg or some eggs from a single fossil clutch, even it is possible to measure the size of eggs from different clutches, but there is a strong constriction: egg must be perfectly preserved, without deformation; otherwise measures could be wrong. Unfortunately, it is not known any perfect clutch of megaloolithid egg, although the completeness of some of them (see Vila *et al*., 2011). Without more tools helping us to evaluate the intra-specific size and shape variation in megaloolithid eggs, it could be assumed the same value of variation (10%) reported in extant reptiles. Therefore, the size and shape of egg may be taking carefully as a diagnostic character for *Megaloolithus* eggs (Fig. 13).

Shell thickness: As occurs in the previous character, shell thickens is subjected to many variable factors. Eggshell formation takes place in a supersaturate solution of ions in uterus, from which growth of crystals occurs (Packard and DeMarco, 1991). The first step of this process consists in fixing of growing crystals in a nucleation center, known as organic core. These crystals, representing

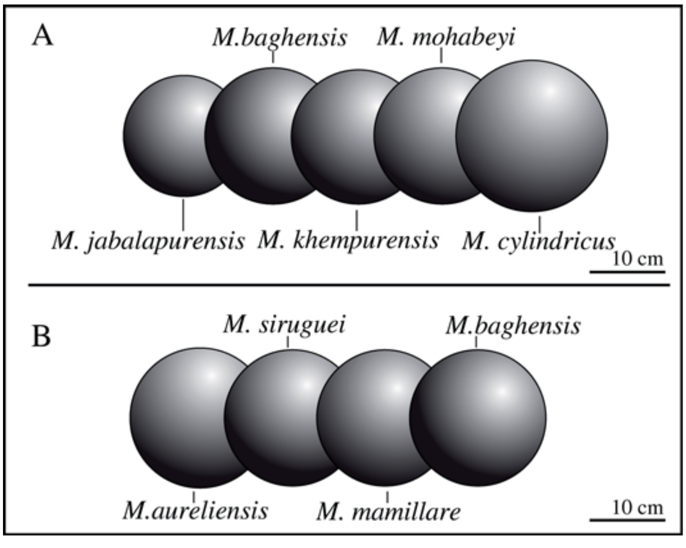

Figure 13. Egg size comparison between different megaloolithid oospecies from A) India and B) Europe.

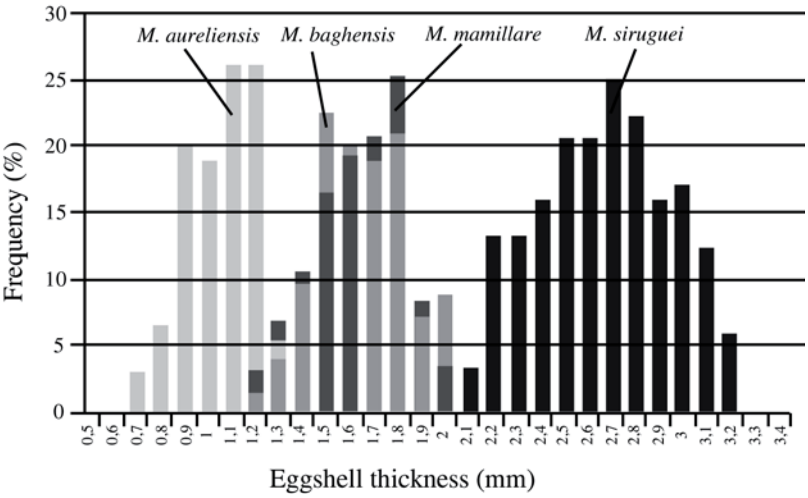

Figure 14. Histogram showing the variability of eggshell thickness in different megaloolithid oospecies.

the germ of shell units, begin to growth laterally. Then, as more additional mineral is deposited on shell units, they come to abut closely and tightly, forming a dense and highly organized calcareous layer (Packard and Hirsch, 1986; Hirsch and Packard, 1987). All this process is guided by hormonal activity, which could have taxonomical implications. However, as is mentioned previously, many factors could intervene in this process. The main constrictor in the shell formation is the amounts of the ionic supersaturate solution, which is composed primarily for calcium ion. In its turn, amount of calcium may depend of resources constriction of the female or even the order of ovoposition, where later eggs are smaller and thinner than first ones (Iverson and Ewert, 1991). In extant turtles, shell thickness also may depend in part on the duration of shell formation (Packard *et al.*, 1984a, b). Intraspecific variation of eggshell in reptile or birds has not been treated by itself, because this factor has been always related with environmental factor (see Blus, 1970; Ratcliffe, 1970; Mathies and Andrews, 2000; Massaro and Davis, 2004, 2005; Castilla *et al.*, 2009; Stewart *et al.*, 2010). But according to data provided by these works, it could be concluded that the shell thickness variation inreptile specie is about 15%-20% (see Packard *et al.*, 1984a, b; Kitimasak *et al.*, 2003). Similar values (12%-15%) have been obtained for megaloolithid eggs from Southern Pyrenees (Panades i Blas, 2005). Thus, it could be assumed a 15% of intra-specific eggshell thickness variation for dinosaur. However, without more structural features helping to identify the oological remain, shell thickness may be takes carefully as a diagnostic character for megaloolithid eggs (Fig. 14).

Ornamental pattern: External ornamentation of eggshell is one of the most valuable external features of the dinosaurian eggshell. Ornamentation represents the expression of the combination of the apical parts of shell units in the outer surface. Therefore, different types of ornamentation are connected with the growing character of the shell unit (Mikhailov, 1991). In this way, it is possible to distinguish three main categories of ornamental surface and its relation with shell units:

1) Smooth surface – The absence of ornamentation is consequence of the flat morphology of the top of shell units. This “ornamentation” can be produced by the headless fan-shape shell unit (as occur in turtles and crocodiles) or by the presence of a thin outer crystalline layer (external layer or cuticle).

2) Rough surface - Ornamentation derived from accretion lines of the single layer, where elements of sculpture cover few shell units. This ornamentation reveals the partial or totally interlocked of shell units, producing irregular relieves.

3) Sculptured surface - Ornamentation connected only with the growth of separate shell units and their subunits. The ornamental elements of sculpture are regular and form a distinct ornamentation pattern. Unlike rough surface, this ornamentation could imply the non fusion between shell units, which are well delimited in lateral view.

This intimate relationship between ornamentation and shell units structure, which could be physiologically and taxonomically controlled (see more detail in Chapter 6), and it could be tentatively used as a good diagnostic character for fossil eggs.

Pore pattern: Pore apertures of eggshell represent the external aspect of the canal pore system in the outer surface. Shape, size and arrangement of pores could reveal information about gas-exchange channel types. Although some patterns seem to be linked to a specific type of egg, different pore system could show similar pore apertures (Mikhailov, 1997). In fact, amount of pore apertures, also known as egg porosity, are mainly related with nesting environment and egg type incubation (Deeming, 2006). For these reasons, the pore pattern cannot be considered as not diagnostic character by itself (but see canal pore system).

Canal pore system: Although our knowledge about the egg formation is higher every day, how pores form is a mystery not solved yet. One hypothesis suggests that threads of protein fibers extend upward from the shell membrane at the site for each pore, and when eggshell is completely formed the threads dissolve leaving the pore behind (Carpenter, 1999). Another idea was proposed by Board (1982), who suggested the presence of fluids between the growing shell units, allowing the formation of pores. A last hypothesis involves the presence of tiny folds of the shell uterine gland, which occur between the developing shell units (Richardson, 1985). However, it is difficult to explain how branched and interconnected pores can be formed by some of these methods. Anyway, formation of pores is controlled for biological and physiological process of female (Deeming and Ferguson, 1991).

But, canal pore system has a very specific function, to allow the gas-exchange between embryo and external environment. It implies that pore system is strongly controlled by physio-environmental requirements (Mikhailov, 1997; Carpenter, 1999; Deeming, 2006; among others). Therefore, although canal pore system is more related with nesting environment than taxonomical influences, this character is important for the description of dinosaur eggshells (Mikhailov, 1997), and it will be used as informative character.

Shell unit: Basic element of eggshell microstructure, and it can be columne-like, skittle-like or barrel-like in shape; prismatic, spherulitic, or homogenous in inner structure (Mikhailov, 1991, 1997). Each high taxonomic group exhibits its own particular shell unit shape, and therefore it can be distinguished between lizards, turtles, crocodiles, dinosaurs and birds (both neognatha and paleognatha). Apparently, it would be not possible to observe significant differences in shell unit between eggs of different species from the same group. But, as it has been observed in modern birds and turtles (Grellet-Tinner, 2000, 2006; Winkler, 2006), the shape of shell units could vary slightly from one species to another. These differences are mainly related with the height/wide ratio and the degree of overlapping or fusion between adjacent units, and they can help to distinguish eggshell from different species. For these reasons, the shape and the fusion of shell units can be accepted as diagnostic features to identify fossil oospecies.

Mammillary size and density: It is well known that eggshell is the major source of calcium for skeletal development in the embryo (Simkiss, 1975; Dieckert *et al.*, 1989; Tuan *et al.*, 1991; Blom and Lilja, 2004). This calcium is removed from the inner part of the shell (mammillary layer), with is located in the organic core (Bond *et al.*, 1988; Board and Sparks, 1991; Karlsson and Lilja, 2008; Blom and Lilja, 2004). In extant birds, growth development of hatchings depend on the size and density of mammillae (Karlsson and Lilja, 2008; Blom and Lilja, 2004; Österström and Lilja, 2011). In precocial birds, mammillary density range from 81% to 55%, while in altricial birds this range is established between 37% to 52% (see Karlsson and Lilja, 2008). Hatchling birds with intermediate state of development (semiprecocial or semialtricial) show a mammillary density from 45% to 57%. Thus, mammillary density informs of embryo development and it is distinctive for each species.

This character has been applied in some fossil eggs, such as theropod eggshells as a diagnostic character to discriminate different oospecies (Varricchio and Jackson, 2004; Zelenitsky and Currie, 2004; Zelenitsky and Therrien, 2008; Jin *et al.*, 2010). Here, it is suggest that the same criteria can be applied to sauropod eggs, considering that the mammillary size and density could be a helpful structural character for to identify different oospecies.

4.2.2. The Megaloolithid Groups (MG'S)

According to criteria mentioned above, three main structural groups within oofamily Megaloolithidae can be distinguished. Each group has their own peculiarities and includes several oospecies. However, some oospecies cannot be included in those structural groups (e.g. *M. maghrebiensis* or *M. problematica*), because they show a unique combination of structural characters and they will be treated individually. Below, each megaloolithid structural group and the possible synonymy between ooespecies is described:

4.2.2.1. Megaloolithid Group 1 (MG1)

Initial composition of MG1 –Three oospecies: *M. jabalpurensis*, *M. dhoridungriensis* and *M. mamillare*.

Description – This group includes thin to mid-thick eggshell megaloolithid oospecies. The oospecies of MG1 normally range from 1 mm to 2.3 mm in thickness, with an average value of 1.7 mm (Fig. 15A, B). Outer surface of eggshell is covered by well distinguished rounded nodes (0.3 mm to 1.3 mm in diameter), which sometime could present coalescences between them (Fig. 15C, D). In lateral view, fan-shape shell units (H/W ratio about 2:1 – 2.5:1) appear well individualized (Fig. 185, B, F), but sometimes can show partial fusions between neighbouring mammillae in groups of two or three eisospherulites (Fig. 15E). Growth lines are well arched throughout whole eggshell. The system of pore canal is composed by slender and narrow funnel-like tubes, corresponding to tubocanaliculate pore system. The structural character for each oospecies included in this group is shown in table 8.

Validity of the oospecies – the MG1 oospecies are easily recognizable by their unique combination of structural characters. Because the differences between these oospecies are minimal, the validity of some of them could be questioned.

Megaloolithus jabalpurensis Khosla and Sahni, 1995:90–91, pl.I, fig. 7; pl. II, figs. 1–4, Fig. 5.

Type Locality – Bara Simla Hill, Jabalpur (Madhya Pradesh,India).

This oospecies is the best known *Megaloolithus* from India. It is represented by hundreds of eggshells and some complete eggs from different sites of Central India (Khosla and Sahni, 1995). Eggshell of *Megaloolithus jabalpurensis* is about 1.0-2.3 mm in thickness and its outer surface is covered by small rounded nodes (0.47 mm in diameter). In radial section, fan-shape shell units are well separate from their neighboring ones by parallel margins. Pore canal is tubocanaliculate and growth lines are well arched throughout eggshell thickness. As was noted by Mohabey (1998) and Vianey-Liaud *et al*. (2003), the generally microstructure of *M. jabalpurensis* is similar to those of *M. mamillare* from France and Spain. In fact, the only clear difference between Indian

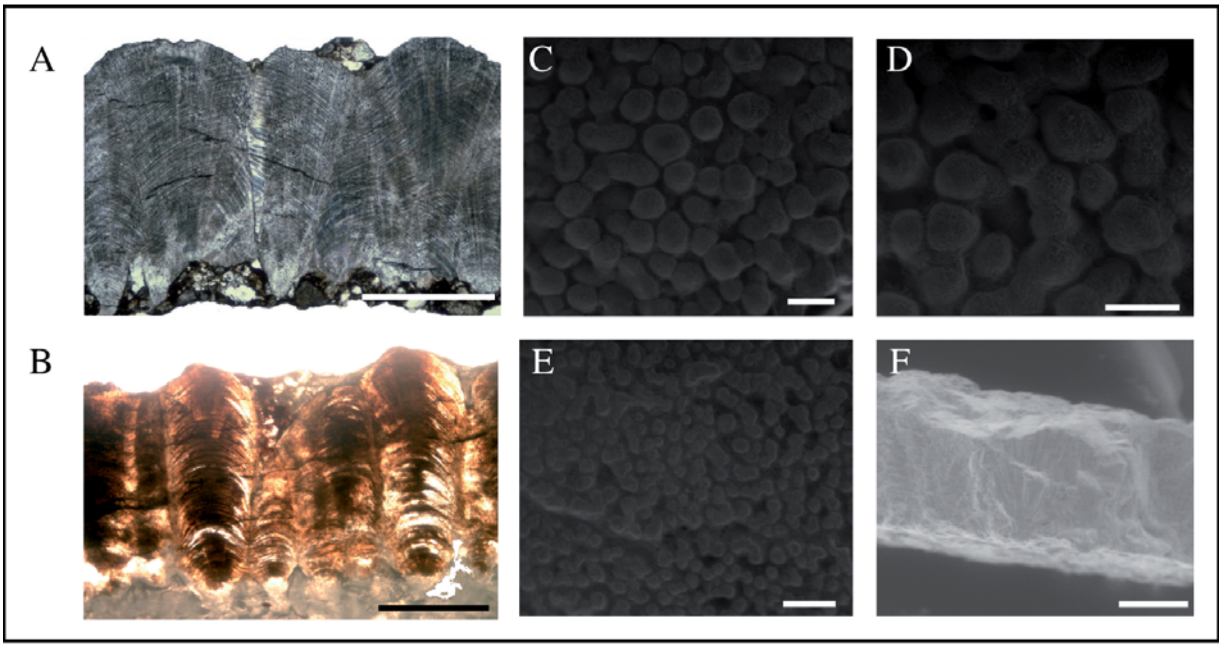

Figure 15. Main structural characters defining the Megaloolithid Group 1 (MG1): (A,B) radial thin section showing individualized fan-shaped shell units of A) *Megaloolithus mamillare* and B) *Megaloolithus dhoridungriensis* (modified from Wilson *et al.*, 2010); (C,D) compactituberculate ornamentation in the outer surface of the shell, with some coalescent nodes; (E) small eisospherulites grouped in the inner part or the shell; (F) SEM micrograph showing a shell units with radial growth of tabular crystals of calcite.Scale bar: 1mm (A,B,F); 0.5 mm (C,D,E).

and European oospecies is the size of eggs, being *M. jabalpurensis* clearly smaller (140–160 mm) than *M. mamillare* (190–230 mm). This difference in size cannot be explained by intra-specific differences. Perhaps, this difference responds to external factors, such as the weather, the resources available or other environment factors. Thus, without more criteria, *M. jabalpurensis* is considered a valid ootaxon.

Megaloolithus dhoridungriensis Mohabey, 1998:352, Fig. 6A–C.

Type Locality – Dhoridungri (Madhya Pradesh, India).

The importance of *Megaloolithus dhoridungriensis* lies in the fact that it is one of the few known eggs with associated embryo of dinosaurs (Wilson *et al.*, 2010). Unfortunately, the brief description reported by Mohabey (1998) does not allow many critical considerations. According to the study made by Vianey-Liaud *et al*. (2003), *M. dhoridungriensis* is nearly identical to *M. jabalpurensis*, just being distinguishable by apparent more slender shell units of *M. dhoridungriensis*. Although rang of thickness of *M. dhoridungriensis* is greater than in *M. jabalpurensis*, values of first oospecies (2.26-2.36 mm) fall within rang exhibited by the second one (1.0-2.38), even some specimens of *M. jabalpurensis* exhibit similar H/W ratio than *M. dhoridungriensis*. Vianey-Liaud *et al*. (2003) also noted how some specimens from Dholiya, firstly determined by Khosla and

Sahni (1995) as *M. jabalpurensis*, would be indeed specimens of *M. dhoridungriensis*. All these observations suggest us that *M. dhoridungriensis* could be considerate as junior synonymous of *M. jabalpurensis*.

Megaloolithus mamillare Vianey-Liaud, Mallan, Buscail and Montgelard, 1994:155-158, Fig. 11.3-8.

Type Locality – Rousset-Erben, (Bouches du Rhône, France).

Megaloolithus mamillare is the type oospecies for the *Megaloolithidus* oogenus. It is represented by hundred of eggs and eggshells from southern France and northern Spain (see Moratalla, 1993; Vianey-Liaud *et al.*, 1994; López-Martínez, 2000; Grigorescu, 2000; Garcia and Vianey-Liaud, 2001 b; Bravo *et al.*, 2005; Vila *et al*, 2011, among others). It is a mid-thick shelled oospecies (1.2-2.1 mm), with relatively large rounded nodes (0.5-1mm in diameter) in its outer surface. Radial view shows well distinguishable fan-like shell units and a tubocanaliculate pore system between them. Growth lines appear well arched and pronounced in whole shell unit. Some basal caps are grouped in clusters containing two or three eisospherulites and forming small chains in the inner surface of the eggshell. As it is mentioned above, *M. mamillare* is very similar to *M. jabalpurensis*, but they differ in the size of egg.

Final composition of MG1 – *M. jabalpurensis* and *M. mamillare*.

Characters	*M. jabalpurensis*	*M. dhoridungriensis**	*M. mamillare*
Egg dimension (cm)	140 - 160	140 - 180	190 - 230
Thickness (mm)	1.0 - 2.38	2.26 – 2.36	1.2 - 2.2
Growth lines	Arched follow surface	Arched follow surface	Arched follow surface
Fused Shell units	Rarely at the base	Rarely at the base	No
Shell units shape	Fan-shaped	Fan-shaped	Fan-shaped
H:W ratio	2.45:1	2.7:1	2:1 – 2.3:1
Node diameter (mm)	0.35-0	unreported	0.3-1.2
Pore diameter (µm)	unreported	unreported	75-120
Mammillae diam. (µm)	0.15 – 0.3	unreported	0.25
Mammillae density (nº/mm^2)	unreported	unreported	unreported

Table 8. Oospecies included in the Megaloolithid Group 1 (MG1). * indicates synonimized oospecies.

4.2.2.2. Megaloolithid Group 2 (MG2)

Initial composition of MG2–Five oospecies: *M. aureliensis*, *M. baghensis, M. petralta, Patagoolithus salitralensis* and *Pseudomegaloolithus atlasi.*

Description – This group includes thin to mid-thick eggshell megaloolithid oospecies. Oospecies from MG2 range from 0.6 mm to 1.7 mm in thickness, with an average value of 1.2 mm (Fig. 16A, B). Outer surface of eggshell is covered by small irregular nodes (less than 0.8 mm in diameter), frequently fused and forming chains. Between chains or isolated nodes there are deep valleys and flat areas of 70-100 µm in wide (Fig. 16C, D). In lateral view, irregular short fan-shape shell units (H/W ratio about 2.3:1) appear frequently fusions between neighbouring ones, being difficult to delimited them (Fig. 16A, B). Relatively big mammillae are also groups in the inner surface of the eggshell (Fig. 16E, F). Growth lines are mainly arched at the base of units but they are undulating throughout whole eggshell. Pore apertures are subcircular in shape (50-150 µm in diameter), and short and narrow pore canals are manly oblique. The structural character for each oospecies from this group is showed in table 9.

Validity of the oospecies – the MG2 oospecies are easily recognizable by their unique combination of structural characters: coalescent nodes and irregular fused shell units.

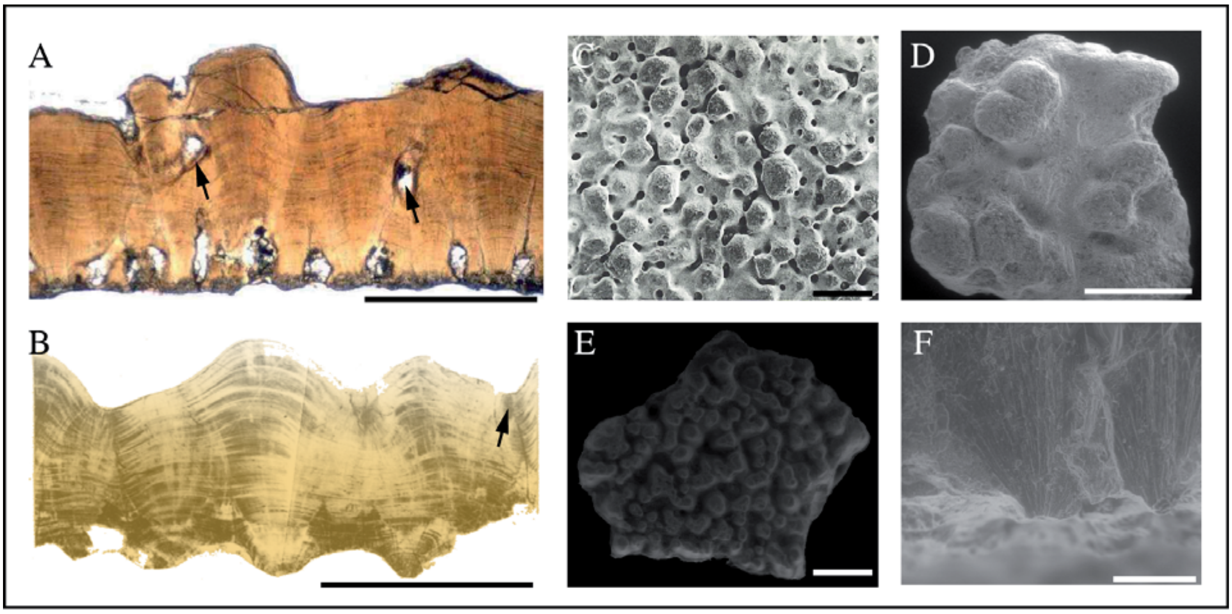

Figure 16. Main structural characters defining the Megaloolithid Group 2 (MG2): (A,B) radial thin section showing fused irregular-fan-shaped shell units of A) *Megaloolithus aureliensis* and B) *Megaloolithus baghensis* (modified from Vianey-Liaud *et al*., 1996), and arrows marks the pore canals; (C,D) compactituberculate ornamentation in the outer surface of the shell, with coalescent nodes and flatted areas between them; (E) small eisospherulites grouped in the inner part or the shell; (F) SEM micrograph showing the base of shell units with radial growth of tabular crystals of calcite. Scale bar: 1mm (A,B); 0.5 mm (C,D,E); 0.300µm (F).

Megaloolithus baghensis Khosla and Sahni, 1995:91–92, pl. II, figs. 5–8; pl. III, Figs. 1, 5.

Type Locality – Bagh Caves (Madhya Pradesh, India).

This oospecies is known from several eggs and eggshells, widely distributed for all the world, being present in Peru, Argentina, Brazil, Spain, France, and India.

Eggshells of *M. baghensis* are 1.0-1.7 mm thick and their external ornamentation consists in coalescent and discrete nodes. Pore apertures are subcircular to elliptical in shape and irregularly distributed in the outer surface. Short and irregular shell units (2.3:1 of H/W ration) appear partially fused in radial view and growth lines are more or less undulating. Pore canals are short, narrow and curve. Relatively wide spherolithes (0.2-0.3 mm in diameter) tent to be grouped which is a characteristic feature of this oospecies (Khosla and Sahni, 1995). Vianey-Liaud *et al*. (2003) synonymised many oospecies to *M. baghensis*, and as it will be showed below, *Patagoolithus salitraensis* and *Pseudomegaloolithus atlasis* should also considered as junior synonymous of *M. baghensis.*

Patagoolithus salitralensis Simón, 2006: 513-528, Fig. 3G-L.

Type Locality – Salitral Moreno in Río Negro province (Patagonia, Argentina)

Eggshell of *P. salitralensis* ranges from 1.05 mm to 1.65 mm in thickness (average of 1.56 mm) and it is covered by small coalescent nodes (0.6 mm in diameter) and irregular isolated ones. Pore openings in the outer surface are subcircular to elliptical in shape and they are 100 µm in their major axis. In radial thin section, irregular fan-shape units appear mostly fused and pore canals are narrow and oblique. Growth lines are horizontal to undulating throughout whole eggshell. The inner surface exhibits small fused mammillae, which are 0.3 mm of diameter. In comparison study made by Simón (2006), author noted many structural similitude between *Patagoolithus*, *M. baghensis* from India and the Peruvian and European *M. pseudomamillare*, currently considered a junior synonymous of *M. baghensis* (Vianey-Liaud *et al*., 2003). The author argued that information reported for those two megaloolithid oospecies was insufficient for to do a confident comparison because, in her opinion, the absence of values about pore dimensions did not allow contrast those oospecies.

Here it is reported all information about *M. baghnesis*, also the values of pore aperture, concluding that *P. salitralensis* named by Simón (2006) and *M. baghnesis* named by Khosla and Sahni (1995) have identical microstructure and, therefore, *P. salitralensis* should be considered as junior synonymous of *M. baghnesis.*

Pseudomegaloolithus atlasis Vianey-Liaud and Garcia, 2003: 176-177, pl. Ig-j, pl. IId-f, Figs 3-4.

Type Locality – Achlouj 2 (Middle Atlas, Morocco).

This African oospecies is known only for few and scattered eggshell fragments from Morocco. The eggshell of *P. atlasis* is thin (0.6-1.14 mm of thick) and it shows irregular nodes and ridges in its outer surface. This ornamentation is complemented by deep valleys and flat areas between those protuberances. *P. atlasis* also exhibit irregular pore apertures, commonly subcirculars, with 70-150 μm of diameter. In lateral view, irregular fan-shape shell units appear interlocked with neighbouring units, and the growth lines are manly undulating. Pore canals displayed for *P. atlasis* are short, narrow and curved. In the inner surface of eggshell, small mammillae are fused in clusters of two to four eisospheruliltes. All characters listed previously are also present in *Megaloolithus baghensis* and in *Patagoolithus salitralensis*. This similitude was also noted by Vianey-Liaud and Garcia (2003), who observed that *P. atlasis* was very similar to oological material from India (*M. baghensis*), Peru and France (*M. baghensis*). In fact, there are no significant differences between Indian and African ootaxa, suggesting that they are the same. For these reasons, *Pseudomegaloolithus atlasis* should be considers a junior synonymous of *Megaloolithus baghensis*.

Megaloolithus aureliensis Vianey-Liaud, Mallan, Buscail and Montgelard, 1994:166-168, Figs. 11.15, ?11.16C-D

Megaloolithus petralta Vianey-Liaud, Mallan, Buscail and Montgelard, 1994:168-171, Fig. 11.16A-B ?C-D

Type Locality – Clos-La-Neuve (Bouches du Rhône, France) for *M. aureliensis* and

Roquehautes-Grand Creux-D (Bouches du Rhône, France) for *M. petralta*.

Here, these two oospecies will be treated together, because as it will shows below their history have been always linked. The main problem with these oospecies is that both megaloolithid "eggs" share many structural characters, such as shell thickness, shape of shell units, growth line shape, ornamental pattern, and nodes and pore diameter and density. The original and brief description of *M. petralta* is really confusing, and it has been changed several times. Initially, *M. aureliensis* was erected based on some ovoid-shaped eggs and bad preserved eggshells, while *M. petralta* was created with few eggshells fragments, both ootaxa occurring in the same stratigraphic levels and sites of France (Vianey-Liaud *et al.*, 1994). French authors noted the great similarity between *M. petralta* and *M. aureliensis*, showing the necessity of more material to validate *M. petralta* oospecies. Later, due to a probable mistake in the description of oological material from Spain, diagnostic characters firstly used for *M. aureliensis* were applied for to re-describe *M. petralta*; mixing characters of both oospecies (see Vianey-Liaud and López-Martínez, 1997). As occurred in French sites, in Fontllonga-6 site (Tremp basin, Spain) one oospecies appeared predominant (?*M. petralta*) over the other (?*M. aureliensis*). Again, both oospecies appeared mixed in same levels within the same site, being difficult to discriminate between them (Vianey-Liaud and López-Martínez, 1997). At this point, these two oospecies were, apparently, identical and for this reason, Carpenter (1999) suggested that both oospecies could be the same. Garcia and Vianey-Liaud (2001) argued that ovoid shape of egg of *M. aureliensis*, which was one of the diagnostic characters for this oospecies (Vianey-Liaud *et al.*, 1994), was consequence of deformation process, being spherical the real shaped of this egg. Due to many microstructural similitudes between both oospecies and according to the scarce oological material referred to *M. petralta* that makes its identification confuse; here, *M. petralta* is considered a junior synonymy of *M. aureliensis*, because this last oospecies was firstly defined (see Vianey-Liaud *et al.*, 1994:166-168 and 168-171, respectively).

Final composition of MG2 – *M. baghensis* and *M. aureliensis*.

4.2.2.3. Megaloolithid Group 3 (MG3)

Initial composition of MG3– Seven oospecies. *M. cylindricus, M. khempuriensis*, *M. megadermus, M. microtuberculata*, *M. mohabeyi*, *M. padiyaliensis* and *M. siruguei*

Description – This group includes mid to thick-eggshell megaloolithid oospecies, including the extremely thick *M. megadermus*, which is up to 4 cm thick. The oospecies of MG3 normally range from 1.8 to 2.6 mm in thickness (Fig. 17A, B, C); even the extreme values have been established in 1.12 mm in *M. padiyaliensis* and 4.8 mm in *M. megadermus*. Outer surface of eggshell is covered by well distinguished rounded nodes (0.9-1 mm in diameter) and rarely there are coalescences between them (Fig. 17D, E). In a cross-section lateral view, cylindrical to fan-shape shell units (H/W ratio about 3:1 - 4:1) appear slender and well individualized. Growth lines are well arched throughout whole eggshell. Very rarely shell units are fused and then growth lines cross them acquiring undulating-shape.

According to own observations, and information reported in the literature (see below), there are two structural characters which could determinate the oological diversity within this group. First character is related with the complexity of the pore canal system and can be exhibited as: 1) simple pore canal or 2) reticulate pore canal (*sensu* Élez and López-Martínez, 2000; Vianey-Liaud and Zelenitsky, 2003). Three oospecies show the simple system (*M. cylindricus*, *M. megadermus* and M. *mohabeyi*) while reticulate pore system is present in three oospecies (*M. khempurensis*, *M. microtuberculata*, and *M. siruguei*) and suggested in one other (*M. padiyalensis*). Second structural character is related with the size and the density of mammillae. As is known

Characters	*M. baghensis*	*Pseudomegaloolithus atlasis**	*Patagoolithus salitralensis**	*M. auleriensis*	*M. petralta**
Egg dimension (cm)	14-20	unknown	unknown	20-22	? 14.5 – 18.5
Thickness (mm)	1-1.7	0.6-1.14	1.05-1.61	0.82-1.52	1.1-1.52
Growth lines	Arched to undulating	Arched to undulating	Arched to undulating	Arched to undulating	Arched to undulating
Fused Shell units	Yes	Yes	Yes	Yes	Partially
Shell unit shape	Short and irregular fan-shape	Short and irregular fan-shape	Short and irregular fan-shape	Short and irregular fan-shape	Short fan-shape
H:W ratio	2.33	≤ 3	2.28	1.75	1.9
Node diameter (mm)	0.63	0.3-0.6	0.8-1.1	0.5	0.4-0.6
Node density (nº/cm^2)	213	unreported	195	262-335	348
Pore diameter (µm)	65-150	70-150	45-175	50-120	65-119
Pore density (nº/cm^2)	185	unknown	170	223	283
Mammillae diam. (µm)	0.2-0.3	unreported	0.3	unreported	unreported
Mamillae density (nº/cm^2)	213	unreported	248	223	347

Table 9. Oospecies included in the Megaloolithid Group 2 (MG2). * indicates synonimized oospecies.

in extant birds, the size and density of mammillae is directly related with osteological development of the embryo and the growth rate of the hatchling (Karlsson and Lilja, 2008; Blom and Lilja, 2004; Österström and Lilja, 2011). For this reason, this character could be important for to distinguish different oospecies. Two subdivisions according to mammillae characters can be done between oospecies of MG3. One subdivision is characterized for exhibit small-size subcircular mammillae (0.07 mm to 0.25 mm in diameter) and pour packed (5-8/mm^2). This subdivision includes *M. padiyalensis, M. mohabeyi, M. megadermus, M. microtuberculata* and *M. siruguei*. The other one is characterized by big-size circular mammillae (0.25 mm to 0.5 mm in diameter) and dense packed (4-12/mm^2). These characters are present in *M. cylindricus* and *M. kempurensis*. In table 10 is specified all structural character of each oospecies.

Validity of the oospecies – As it is showed above, MG3 is the structural group that contains more ootaxa. However, some structural criteria used by distinguish each oospecies from other should be questionable, and other ones should be reinterpreted. Following, it is discussed the validity of all megaloolithid oospecies included in MG3, and first will be treated the valid oospecies.

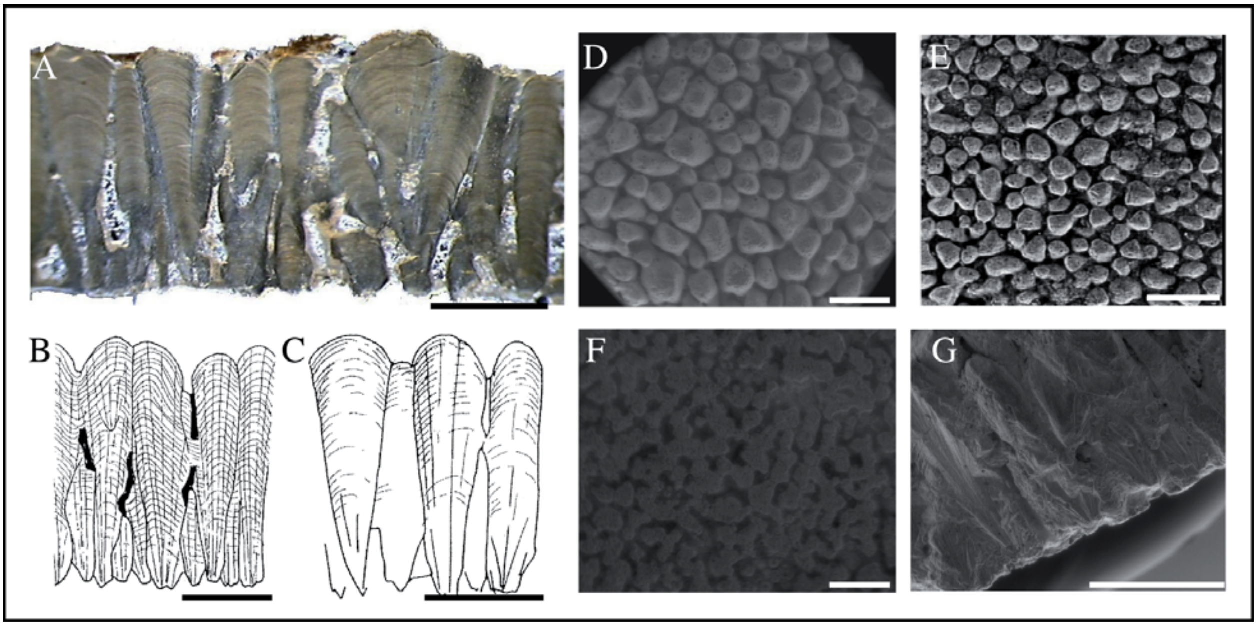

Figure 17. Main structural characters defining the Megaloolithid Group 3 (MG3): (A,B,C) radial thin section showing individualized long-fan-shaped shell units of A) *Megaloolithus siruguei*, B) *Megaloolithus microtuberculata* (modified from Garcia and Vianey-Liaud, 2001a) and C) *Megaloolithus cylindricus* (modified from Vianey-Liaud *et al*., 2003); (D,E) compactituberculate ornamentation in the outer surface of the shell in D) *Megaloolithus siruguei* and E) *Megaloolithus microtuberculata*; (F) small eisospherulites grouped in the inner part or the shell; (F) SEM micrograph showing the base shell units with radial growth of tabular crystals of calcite. Scale bar: 2mm (A,B,C); 1mm (D,E); 0.5mm (F,G).

Megaloolithus cylindricus Khosla and Sahni, 1995:89–90, pl.1, Figs. 1–6, Fig. 5.

Type locality – Chui Hill in Jabalpu district (Madhya Predesh, India).

This oospecies in represented by tens of complete eggs and abundant eggshell fragments from many sites of India (Khosla and Sahni, 1995; Mohabey, 1998; Vianey-Liaud *et al*., 2003). As thicker as *M. siruguei*, *M. cylindricus* is characterized by to exhibit slender cylindrical-shape shell units, well formed rounded ornamental nodes and a simple tubocanaliculate pore system. This Indian oospecies differs from *M. siruguei* and M. *khempurensis* in the pore system type and from *Megaloolithus mohabeyi* in the size of the mammillae.

Megaloolithus khempurensis Mohabey, 1998:351–352, Fig. 5G–K.

Type locality – Khempur and Werasa in Kheda district (Gujarat, India).

M. khempurensis is known for several eggs and eggshells debris from western India (Mohabey, 1998: Vianey-Laiud *et al*., 2003). The main characters of this oospecies are the well distinguishes cylindrical-shape of the shell units, ornamental nodes sometimes fused and raticulate pore system. Then, *M. khempurensis* differs from *M. cylindricus* and *M. mohabeyi* in the type of canal pore system and from *M. siruguei* by the size of the mammillae, being the bigger of the Indian oospecies.

Megaloolithus mohabeyi Khosla and Sahni, 1995:91, pl. I, Fig. 8, Fig. 5.

Type locality – Hathni River Section, Dholiya in Dhar district (Madhya Predesh, India).

This Indian oospecies is the thinner of megaloolithid oospecies; being the thickness of its eggshells about 1.8-1.9 mm. *Megaloolithus mohabeyi* exhibits cylindrical to slender fan-shaped shell units, which rarely are fused. Outer surface is covered of rounded nodes. Canal pore system of *Megaloolithus mohabeyi* has been interpreted as tubocanaliculate (Vianey-Liaud *et al*., 2003), even it shows some expansion in the middle part of canals, which have been interpreted as consequence of diagenetic process (Khosla and Sahni, 1995; Vianey-Liaud *et al*., 2003). Finally, *Megaloolithus mohabeyi* differ from *M. siruguei* and *M. khempurensis* in the pore system type and from *M. cylindricus* in the size of the mammillae.

M. siruguei Vianey-Liaud, Mallan, Buscail and Montgelard, 1994:162-166, Figs. 11.11, 11.12, 11.13A, 11.14.

Type locality – La Bégude (Bouches du Rhône, France).

Megaloolithus siruguei is one of best knownf megaloolithid eggs. It is represented by hundreds of eggs and eggshells (Moratalla, 1993; Vianey-Liaud *et al.*, 1994; López-Martínez, 2000; Grigorescu, 2000; Garcia and Vianey-Liaud, 2001b; Bravo *et al.*, 2004, 2005; Vila *et al*, 2011; in Chapter 5, among others) and clutches (Vila *et al.*, 2010c), which have been found in France, Spain and Rumania. This oospecies is characterized by to show a relatively thick eggshell (1.8-3.2 mm in thickness); well developed comapctituberculate ornamentation in outer surface of the eggshell; well distinguished slender fan-shape shell units, rarely fused; a reticulate canal pore system; and small mammillae. It differs from *Megaloolithus cylindricus* and *Megaloolithus mohabeyi* in the shape of shell units and pore system and from *Megaloolithus khempurensis* in the size of mammillae.

Below, some oospecies will be reinterpreted while others must be reconsidered as invalid ootaxon or junior synonymous :

Megaloolithus megadermus Mohabey, 1998:353–357, Figs. 3F, 7A–G.

Type Locality – Dholidanti in Panchmahals district (Gujarat, India).

Megaloolithus megadermus is the thickest megaloolithid egg known in the world. This oospecies is known for few eggs and some eggshells from the Maastrichtian Lameta Formation. As it is mentioned previously, *M. megadermus* is two times thicker (4 mm) than other megaloolithid oospecies (frequently, less than 2 mm, and its H/W ratio (9.6:1) is also two or three times bigger than any other *Megaloolithus* known. In fact, this unique condition is considered the diagnostic character for this Indian oospecies. Unfortunately, no samples of *M. megadermus* have arranged for to do an exhaustive study about this oospecies.

Interestingly, Mohabey (1998: 353-357, Fig. 3F, 7A-G) said: “The shell units have grown irregularly in competence with each other and show interfering growth. Extra growth centres are common in the interstices” and conclude that “The extra growth centres and the chaotically growth giant and dwarf shell units may suggest abnormality in the process of the eggshell formation.” Similar thick eggshells have been found in La Tejera site (Burgos province, Spain) (Bravo *et al.*, 2004). Many of those eggshells range from 2.32 mm to 2.9 mm in thickness, but 40% of those eggshells are 5.4 mm thick and 4% are extremely thick (6.6-7.5 mm). Thin sections reveal than those megaloolithid eggs from Burgos show pathological process, such a double growth development of eggshells, phenomena known as “*ovum in ovo*”. This pathology seems to be relatively common in the oological record, being reported in other fossil eggshells (Zelenitsky and Hills, 1997; Jackson *et al*, 2002; Jackson and Varricchio, 2003; Jackson, 2007).

From a biological point of view, an extremely thick eggshell must need some structural requirements which allow the correct development of the embryo within the egg. One of these important conditions is related with gas-exchange. The eggshell must promote proper gas exchange between inside and outer environments of eggs, and this objective is only accomplished with a good canal pore system (Ar *et al.,* 1974; Deeming and Ferguson, 2004; Deeming, 2005). In thick eggshells (up to 2 mm) this task is possible if the canal pore system is composed by a complex network of gas-exchange canals, allowing the correct oxygen supply and carbonate dioxide evacuation (Figueroa and Powell, 2000). For example, the eggshells of ancient bird *Aepyornis* and extant ostrich, which are 1.7mm to 3.1 mm in thickness, pores are subdivided into multibranching canals throughout the shell (Mikhailov, 1991, 1997; Grellet-Tinner 2000), optimizing the gas flux. Similar solutions are present in some fossil eggs, such as in *Megaloolithus siruguei* (Vianey-Liaud *et al*., 1994) and in *Faveoloolithus* (Zhao and Ding, 1976), which show reticulate or multicanaliculate pore systems. If *M. megadermus* was a "real" thick-shelled oospecies) then it might show some kind of pore canal adaptation, like multibranching canals. But surprisingly, this character is not present in the Indian *Megaloolithus*, which shows a simple tubular pore system, being an inappropriate structure for the development of embryo.

Concluding, if the diagnostic characters (extremely thick eggshell) of *M. megadermus* are consequence of pathology and the pore system exhibit for this oospecies is not appropriated for such thick eggshells, then *M. megadremus* must be considerate an invalid ootaxon.

Megaloolithus padiyalensis Khosla and Sahni, 1995:93–94, pl. IV, Figs. 5–6, Fig. 5.

Type locality – Padiyal in Dhar district (Madhya Predesh, India).

The Indian oospecies *Megaloolithus padiyalensis* is known for few eggshell fragments, which have been found in the Lameta Formation, and it appears frequently associated to *M. mohabeyi* in the same sites (Khosla and Sahni, 1995). In their review about Indian megaloolithid oospecies, Vianey-Liaud *et al*. (2003) noted eggshells of *Megaloolithus padiyalensis* exhibits microstructural characteristics similar to those of *M. mohabeyi*, but the shell units of *M. padiyalensis* display various lengths and widths and are often fused laterally, characters not present in *M. mohabeyi*. They also noted that the eggshells of *M. padiyalensis* are generally eroded, and the pore canals are somewhat enlarged by recrystallizations, evidencing the poor preservation of this oospecies. If the diagnostic characters used by Khosla and Sahni (1995) to define *M. padiyalensis* are considered, the thickness and the irregular pore canals are result of diagenetical processes, then *Megaloolithus padiyalensis* must be considerate an invalid ootaxon. Even more, due to microstructural similarities between *M. padiyalensis* and *M. mohabeyi* and their co-occurrence in the same levels and sites, *M. padiyalensis* could represents alternated specimens of *M. mohabeyi.*

Megaloolithus microtuberculata Garcia and Vianey-Liaud, 2001: 187-188, Fig. 1.

Type locality – La Cairanne (Bouches-du-Rhône, France).

Until now, *M. microtubercultada* has been only reported in a single level of a single site in France. Garcia and Vianey-Liaud (2001) found five partial eggs in red marls of La Cairenne site, the outer surface of which was ornamented whit relatively small nodes (0.2-0.6 mm in diameter), character that gives the name to this oospecies. Microstructure of *M. microtuberculata* is very similar to *M. siruguei*, both oospecies shared the same range of thickness and pore diameters; even so they exhibited a similar reticulate pores system pattern. Although, Garcia and Vianey-Liaud (2001) suggested that minor size of egg (16 cm in diameter) and ornamental nodes showed by *M. microtruberculata* were enough distinctive characters to differentiate this oospecies from *M. siruguei*. In our own opinion, these criteria are no really strong and they would be considered as intra-specific variations.

In one hand, *M. mictrotuberculata* is known by little material, including five partial and broken eggs. The size of egg given for this oospecies was taken from a crashed and compressed egg (see Garcia and Vianey-Liaud, 2001a: Fig1.1), therefore the value reported would not represents the real dimensions of the entire egg. Even without taking into account this condition, as it is mentioned previously, the size of egg of current amniotes can change up to 10% as consequence of intra-specific variation. According to observation made by Garcia and Vianey-Liaud (2001a), microstructure of *M. microtuberculata* is extremely similar to *M. siruguei*. Typically, eggs of *M. siruguei* ranges from 19 cm to 23 cm in diameter, but some specimens have only 17 cm of diameter, representing the 10% of intra-specific variation. This last value is coherent with the size reported for *M. microtuberculata*. In this way, it would imply that *M. microtuberculata* could represent a small size *M. siruguei* egg.

The second diagnostic character of *M. microtuberculata* is the size of nodes, which are smaller than in *M. siruguei* (Garcia and Vianey-Liaud, 2001a). The size of nodes depends of the size (width) of shell units, because nodes are the apical part of these crystalline units and, in its turn, sizes of shell units are directly proportional to eggshell thickness (Mikhailov, 1997). In other words, the size of nodes depends on the eggshell thickness. For this evaluation eggshells of *M. microtuberculata* from La Cairenne site, *M. siruguei* from La Bégude site (both courtesy of Monique Vianey-Liaud) and eggshells *M. siruguei* of from Coll de Nargó and Tremp Basin are used. According to own observations, the size of ornamental nodes is directly proportional to the thickness of the eggshell, where eggshells of *M. siruguei* as thick as *M. microtuberculata* show similar size of nodes in both oospecies. Then, it would suggest that the small size of nodes in *M. microtuberculata*, which is considered as a diagnostic character, is consequence of the minor thick of the eggshell exhibit by this

Characters	*M. cylindricus*	*M. megadermus*[*]	*M. siruguei*	*M. microtuberculata*[*]	*M. mohabeyi*	*M. padiyaliensis*[*]	*M. khempuriensis*
Egg dimension (mm)	120 - 200	130 - 180	170-230	160	160 - 190	Unknown	170 - 200
Thickness (mm)	1.7 - 3.5	4.0 – 4.8	2.2 – 3.2	1.8 – 2.5	1.8 - 1.9	1.12 – 1.68	2.36 – 2.6
Growth lines	Arched	Arched	Arched	Arched	Arched	Arched	Arched
Fused Shell unit	No	No	Rarely the upper part	Rarely the upper part	No	No	No
Shell unit shape	Conic-shaped	Conic-shaped	Fan-shaped	Fan-shaped	Conic-shaped	Conic-shaped	Conic-shaped
H:W ratio	4:1	9.6:1	4:1	3.6:1	3.1:1	3.95:1	2.9:1
Node diameter (mm)	0.8-1.0	unreported	0.4-1.1	0.3-0.6	0.6-0.9	0.4-0.7	0.6-0.8
Node density (nº/cm^2)	unreported	unreported	265	465	unreported	unreported	unreported
Pore diameter (µm)	unreported	unreported	50-80	25-120	60-80	unreported	50 - 90
Canal pore system	Tubocanaliculate	Tubocanaliculate	Reticulate	Reticulate	Tubocanaliculate	Ttubocanaliculate	Reticulate
Mamillae diameter (µm)	0.2 - 0.5	unreported	0.15-0.2	0.12-0.18	0.14 – 0.21	0.07 - 0.21	0.25 – 0.3
Mamillae density (nº/cm^2)	4-12	unreported	5-8	5-7	5-9	5-8	5-16

Table 10. Oospecies included in the Megaloolithid Group 3 (MG3). * indicates non valid or synonimized oospecies.

oospecies.

For all these reasons, it is suggest that there are not significant differentials between these two oospecies and, for this, *M. microtuberculata* could be considers as a junior synonymous of *M. siruguei*.

Final composition of MG3 – *M. siruguei*, *M. mohabeyi*, *M. kempuriensis* and *M. cylindiricus*

4.2.2.4. Ungrouped megaloolithid oospecies

Oospecies of *Megaloolithus* by whose comvination of structural characters can not be included in any of previous groups are listed below:

Megaloolithus maghrebiensis Garcia, Tabuce, Cappetta, Marandat, Bentaleb, Benabdallah and Vianey-Liaud, 2003:62-63, pl. I, Fig. 2d-e.

Type locality – Achlouj 2 (Middle Atlas, Morocco).

M. maghrebiensis is the most common megaloolithid eggshell in North Africa (Garcia *et al*., 2004; Vianey-Liaud and Garcia, 2004) and it is known for hundreds of eggshells from the Upper Maastrichtian in Morocco. This oospecies seems to mix characters of all megaloolithid groups described before. In one hand, its eggshells are so thick (2.2 mm in average) as *M. mohabeyi* from the MG3 and its external ornamentation resemble those *M. jabalpurensis* and *M. mamillare* from the MG1, but some nodes are fused together as in *M. baghensis* from the MG2. In lateral view, shell units are slender as occur in *M. mohabeyi* and *M. siruguei* from the MG3, but frequently they are partially fused whit adjacent shell units as in megaloolithids from the MG2. *M. maghrebiensis* also share with this last group the obliquity of pore canals and their elliptical shape in outer surface. Nothing is mentioned about the size or fusion of mammillae. Apparently, this oospecies seems a middle state between megaloolithid eggs from the MG2 and MG3. No other *Megaloolithus* display this unique combination of characters, and for this reason it is consider *M. maghrebiensis* a valid ootaxon.

Megaloolithus problematica Mohabey, 1998:358, Fig. 3H, Fig. 8C-E.

Spheroolithus problematica nov. com.

Type locality – Balasinor in Kheda district (Gujarat, India).

This "megaloolithid" egg has been largely forgotten, being reported in the literature only two times (Mohabey, 1998, 2000). *M. problematica* was described by Mohabey (1998) base in some partial eggs and some eggshells fragments. This ootaxon was very different from the other *Megaloolithus* from India and Europe. Eggs of *M. problematica* are spheroidal in shape (17.5x14 to 15x12 cm in diameter) with ramotuberculate ornamental patter in the outer surface of the eggshell and it exhibits a prolatocanaliculate pore system, while all known *Megaloolithus* have spherical eggs with compactituberculate ornamentation and tubocanaliculate pore system. Although Mohabey (1998) questioned the parataxonomical assignation of this ootaxon to Magaloolithidae, he never contemplated the option to attribute *M. problematica* to any other oofamily. A brief revision of the material (Mohabey, 1998:358, Fig. 8C-E) has allowed us to make new consideration about this enigmatic ootaxon.

According to original description, *M. problematica* exhibits some structural characters not in accordance with megaloolithid eggs. Apart of structural characters listed above for *M. problematica*, shell units are frequently fused in this ootaxon. The combination of these characters is commonly attributed to prolatospherulitic morphotype (Mikhailov, 1997). To date, only type of fossil egg is attached to this morphotype, *Spheroolithus* (Zhao, 1979; Mikhailov, 1997). In fact, many structural characters displayed by *M. problematica* are present in *Spheroolithus choteauensis* (Jackson and Varricchio, 2010). Therefore, here it is suggested *M. problemantica* could be considered a *Spheroolithus* oospecies and it must change its name for *Spheroolithus problematica* nov. com.

In table 11 is compared the number of valid ootaxa belonging to Megaloolithidea oofamily, after and before of critical revision showed herein.

	BEFORE RE-VIEW		AFTER RE-VIEW	
OOFAMILY	**OOGENERA**	**OOSPECIE**	**OOGENERA**	**OOSPECIE**
MEGALOOLITHIDAE	*MEGALOOLITHUS*	*aureliensis*	*MEGALOOLITHUS*	*aureliensis*
		baghensis		*baghensis*
		cylindricus		*cylindricus*
		dholiyaensis		*dholiyaensis*
		dhoridungriensis		*jabalpurensis*
		jabalpurensis		*khempurensis*
		khempurensis		*maghrebiensis*
		maghrebiensis		*mamillare*
		mamillare		*mohabeyi*
		megadermus		*siruguei*
		microtuberculata		**TOTAL: 10**
		mohabeyi		
		padiyalensis		
		petralta		
		problematica		
		siruguei		
	? CAIRANOOLITHUS	*doughii*		
		roussetensis		
	PSEUDOMEGALOOLITHUS	*atlasi*		
	PATAGOOLITHUS	*Salitraensis*		
		TOTAL: 20		

Table 11. Comparison between oospecies quipped valid before and after the study review.

4.3 MEGALOOLITHID EGGS IN THE UPPER CRETACEOUS OF SOUTHERN PYRENEES FROM CATALONIA

Although previous paleontological works about dinosaur eggs performed in Southern Pyrenees suggested the presence of diverse oospecies of *Megaloolithus* (e.g. five according to Vianey-Liaud and López-Martínez (1997) or six, *sensu* Escuer *et al*. (2006)), according to our own observations and criteria it would be possible to identify four megaloolithid oospecies in the Upper Cretaceous of South Pyrenees from Catalonia. These oospecies are described below.

4.3.1 Systematic Paleontology

VETEROVATA Vialov, 1972

Organization group: Dinosauroid

Structural morphotype: Discretispherulitic

Oofamily MEGALOOLITHIDAE Zhao, 1979

Oogenus *Megaloolithus* Vianey-Liaud, Mallan, Buscail and Montgelard, 1994.

Megaloolithus aureliensis Vianey-Liaud, Mallan, Buscail and Montgelard, 1994. Diagnosis emended by Garcia and Vianey-Liaud (2001a).

Material - 13 eggshell fragments (ISP-59099) from an isolated egg from Coll de Nargó (Alt Urgell) and 15 eggshell fragments (ISP-58959) from Blancafort site (La Noguera).

Description - Eggshells from Coll de Nargó Syncline are relatively thin (1.11-1.44 mm in thickness) with an average value of 1.19 mm, while those from Blancafort are somewhat thinner (0.8 to1.2 mm of thick). The outer surface appears slightly weathered and covered with widely separated nodes which sometimes can be fused. When nodes are well developed they can reach up to 0.1 mm in height and 0.5 mm of diameter and frequently appear in group of two or three nodes, forming chains (Fig. 18A.2). In radial thin section, eggshell units are fan-shaped (Fig. 18A.1), with a H/W ratio about 2.32, and commonly fused with adjacent ones in 2/3 parts of the total shell unit thickness. Growth lines are more or less curved and continue between fused units (Fig. 18A.3). The pore system is of the tubocanaliculate type with a canal of 90-130 µm in diameter (Fig. 18A.3), while the ovoid to circular-shaped pores apertures are 80-170 µm in diameter. In some specimens from Coll de Nargó Syncline, the inner surface shows some patches of fibrous calcified layer of 0.3 mm thick covering the mammillae (Fig. 18E.1).

Discussion – Structural character exhibit by this type of eggshell could be referred to *M. aureliensis* or *M. petralta*. As it was exposed in Chapter 4.1.2, both oospecies share a lot of structural characters, like shell thickness, growth line shape, ornamental pattern, node and pore diameter and density. According to discussion provided in previous chapter and agree with the tentative synonymy between these two oospecies, considering *M. petralta* as junior synonymous of *M. aureliensis*, these eggshells from Coll de Nargó and Blancafort site could be referred to *Megaloolithus aureliensis*.

This oospecies was reported previously from Fontllonga-6 site (Vianey-Liaud and López-Matrínez, 1997) and Moror (López-Martínez, 2000), both sites in Àger Syncline, and in Pinyes site (Escuer *et al*., 2006) in Coll de Nargó Syncline.

Megaloolithus siruguei Vianey-Liaud, Mallan, Buscail and Montgelard, 1994

Remarks - Original diagnosis of the oospecies was partially modified and completed by Élezlez and López-Martínez (2000), and Vianey-Liaud and Zelenitsky (2003).

Material - More than 400 eggshell fragments taken from several clutches in consecutive stratigraphic levels (IPS-58994 to IPS-59013; IPS-59017 to IPS-59072; IPS-5979 to IPS-59098; IPS-59100 to IPS-59103), 563 eggshell fragments from different stratigraphic levels (IPS-59195 to IPS-59115), all them from the Coll de Nargó Syncline (Alt Urgell); 102 eggshell fragments (ISP-58966) from Barranc de la Fonguera and Biscarri sites (Pallars Jussà)

Description - Eggs are spherical in shape (19 to 21 cm in diameter). The outer surface is completely covered with rounded nodes which constitute the top of the spherulitic shell units (compactituberculate ornamentation), with a diameter of 0.51-1.23 mm (Figs. 18B.2). The rounded-shaped pore openings are 0.13 mm in diameter and they are located between and rounding the ornamental nodes. The eggshell thickness ranges from 1.75 to 3.6 mm in Coll de Nargó and from 1.68 to 3.24 mm in the Pallars Jussà sites. The elongated fan-shaped shell units are four to five times higher than wide and well distinguished. The discrete shell units are composed of radiating calcite crystals; and rarely some degree of fusion between units occurs (Fig. 18B.1). The growth lines are curved from the base to the top of the units and continue through adjacent units. The pore canals are more or less straight (diameter range from 40 to 130 μm) and interconnected by transversal ones thus forming a three-dimensional network which is characteristic of this oospecies (Fig. 18B.3). The inner surface shows rounded and tightly packed mammillae which are united forming small chains and, sometimes, they are covered by an irregular fibrous calcified layer (Fig. 18E.2).

Discussion - Three megaloolithid oospecies have a three-dimensional pore system: *M. siruguei*, *M. microtuberculata* and possibly *M. padiyalensis* (Vianey-Liaud and Garcia, 2000; Vianey-Liaud *et al.*, 2003). These oospecies differ mainly in eggshell thickness although the ranges overlap, thus *M. siruguei* has a thickness range between 1.7–3.2 mm, *M. microtuberculata* between 1.84-2.52 mm and *M. padiyalensis* from 1.12-1.68 mm (Garcia and Vianey-Liaud, 2001a; Vianey-Liaud *et al.*, 2003). The eggshells from Coll de Nargó are thicker than *M. padiyalensis* but they fall within the range of *M. microtuberculata*. *M. siruguei* and *M. microtuberculata* also differ in the morphology and node dimensions. *M. siruguei* nodes are rounded, with a diameter between 0.4-1.1 mm (Vianey-Liaud *et al.*, 1994) and a node density of 265 nodes/cm^2. *M. microtuberculata* nodes are more irregular in shape and smaller (diameter between 0.19–0.6 mm and 465 nodes/ cm^2) (Garcia and Vianey-Liaud, 2001a). The quantitative characters of the eggshells of Coll de Nargó site agree better with those of *M. siruguei* (node diameter 0.15–1.23 mm and density of 240 nodes/cm^2). In their revision of the megaloolithid oospecies from France and India, Vianey-Liaud and collaborators (2003) noted the strong similarities between *M. microtuberculata*, *M. siruguei* and *M. cylindricus* although they maintain these oospecies based on quantitative differences. The variability of the quantitative characters of megaloolithid eggshells have been early recognized (Mikhailov, 1997b) but they are not yet fully explored. The main diagnostic character of *M. siruguei* is the presence of a three-dimensional respiratory canals system and probably it should be considered as a unique and derived character and then, the three former oospecies can be synonymized (see more details in Chapter 4.1.2).

Megaloolithus siruguei is the most common megaloolithid oospecies in the Upper Cretaceous of South Pyrenees of Catalonia, being present in Biscarri (Moratalla, 1993; López-Martínez, 2000); Coll de la Faidella (also Barranc de la Fonguera)(Bravo *et al.*, 2000); Pinyes site (Escuer *et al.*, 2006; Jackson et la., 2008; Vila *et al.*, 2010c) and Vallcebre Syncline (Bravo *et al.*, 2005; Vila *et al.*, 2011).

Megaloolithus mamillare Vianey-Liaud, Mallan, Buscail and Montgelard, 1994.

Material – 101 eggshell fragments from Tossal de St. Romà site (ISP-58963), 109 fragments from Costa de la Coma (IPS-58964), and 36 eggshells from Els Nerets (ISP-58965) (Pallars Jussà).

Description – Frequently, sub-spherical eggs about 19-20 cm in diameter. The shell of those eggs range from 1.39 to 2.3 mm in thickness (average of 1.9 mm). Their outer surface is covered by small rounded nodes of 0.73 mm in diameter, sometimes with coalescences of two to five nodes, forming short and irregular ridges (Fig. 18C.2). In radial thin section, fan-shaped shell units are discrete, and two times high than wide, showing curved growth lines from the base to the top of the crystalline units (Fig. 18C.1). The respiratory system is tubocanaliculate, with narrow and slender canals ranging from 50 to 80 µm in wide. The inner surface appears covered by rounded packed mammillae (Fig. 18C.3)

Discussion – *Megaloolithius mamillare* is distinguished by showing not fused wide fan-shaped units and some coalescent nodes in the eggshell surface. However, two other megaloolithid oospecies could coincide with described material: the Indian *Megaloolithus jabalpurensis* and the Argentine *Megaloolithus patagonicus*. Vianey-Liaud *et al.* (2003) observed the high similitude between these three oospecies of *Megaloolithus*, proposing to group them within the same structural pattern; even proposed a synonymy between *M. jabalpurensis* and *M. patagonicus*. Even so, *M. jabalpurensis* is somewhat thicker than *M. mamillare* (2.3 mm and 2.1 mm, respectively) and Indian and Argentinean megaloolithid eggs are smaller in size (14-16 cm in diameter) than European megaloolithid oospecies (19-23 cm in diameter) (see more details in Chapter 4.1.2). Eggs from Tremp Basin are 19-20 cm in diameter and their eggshells are 1.9 mm in thickness; for these reasons this oological material is referred to *Megaloolithus mamillare*.

As occurred with *M. siruguei*, *M. mamillare* is a common oospecies in the Maastrichtian continental deposits of South Pyrenees, being reported from Basturs, Suterranya, Abeller and Comportas sites in the Tremp Basin (Moratalla, 1993; Sanz, *et al.* 1995; Vianey-Liaud and López-Martínez, 1997; Peitz, 2000b; Sander *et al.*, 2008) and Torrent de l'Esdavella and Els Terrers in the Vallcebre Syncline (Vila *et al.*, 2011).

Megaloolithus baghensis Khosla and Sahni 1995

Material - 8 eggshell fragments (IPS-59014) from two partial eggs in Coll de Nargó Syncline in Alt Urgell. In the Pallars Jussà county, 90 eggshell fragments from Barranc de la Boïga (IPS-58960); 25 eggshells from Abella site (IPS-58967); 17 eggshell fragments from Suterranya (IPS-58968); 50 eggshell fragments from Molí del Baró (IPS-58975); 1 eggshell from Serrat del Rostiar site (IPS-58982); 50 fragments from Camí del Soldat site (IPS-58987); finally, in the La Noguera county, 8 eggshell fragments from l'Espinau site (IPS-58992).

Description - Eggs found in Suterranya are subspherical to ovoid in shape. The smallest egg is 15-18 cm in diameter, while the largest is 21-23 cm, like in Coll de Nargó. The outer surface is covered by coalescent rounded nodes ranging 0.2 to 0.6 mm in diameter. However, some nodes appear isolate and flat areas extend between nodes. Pore opening are 0.1-0.2 mm in diameter and are located in the middle of flattered areas. The eggshell thickness ranges from 1.12 to 1.85 mm, with an average of 1.39 mm. Eggshell units are short, broad and fan-shaped (H/W ratio about 1.88), frequently fused with adjacent units (Fig. 18D.1). When units are fused they show irregular morphology in their upper part. Outer surface appears partially covered with rounded nodes, which are frequently lesser than 0.5 mm of diameter and sometimes are fused with adjacent ones (Fig. 18D.2). In radial thin section, the pore canals are funnel-like, wider in their upper part, as corresponds to tubocanaliculate pore system (Fig. 18D.3). Also in radial view, growth lines appear slightly arched from the base to the top of the shell-units and continuous between fused adjacent units. However, when outer surface is smooth, growth lines are horizontal or slightly undulated. Tubocanaliculate system can be observed between shell units. These canals are narrow and 0.075 mm in wide. The inner surface shows a packed mammillae (0.25-0.3 mm in wide) fused, forming small chains. In some eggshells, a thin layer about 0.3 mm thick is attached to the base of the shell units (Fig. 18D.3, 18E.3).

Discussion – The thickness and the general shape of shell units observed in our material resemble those *Megaloolithus mamillare*, but our eggshells differ from this last oospecies in the fusion of shell units, the

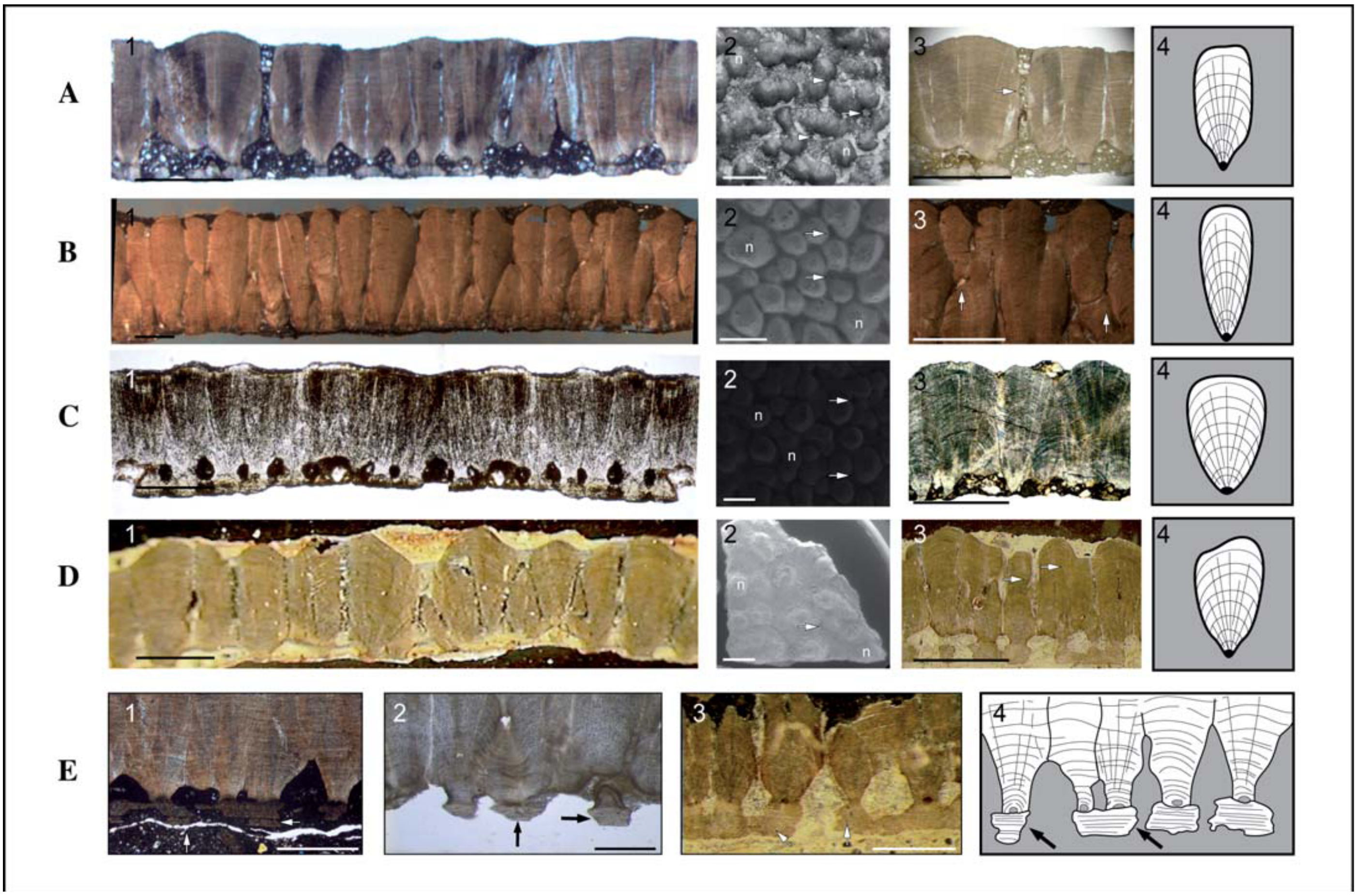

Figure 18. Megaloolithid oospecies from South-Central Pyrenees: A) *Megaloolithus aureliensis,* B) *Megaloolithus siruguei*, C) *Megaloolithus mamillare* and D) *Megaloolithus baghensis*. For each oospecies and from the left to the right: 1) Radial section showing the principal microsctructural characters, 2) the outer surface ornamentation, 3) detail of respiratory canals and 4) morphological scheme of eggshell-units. (E) Some examples of fossil eggshell membrane in: 1) *M. aureliensis*, 2) *M. siruguei*, 3) *M. baghensis*, and 4) a schematic draw made with camara lucida. Arrows point the situation of pore apertures (in 2), respiratory canals (in 3) and the eggshell membrane (in F). n – nodes. Scale bar: 1mm

coalescence of ornamental nodes and the pore canal shape. Base on fragmentary elements recovered from different countries; Vianey-Liaud *et al*. (1997) described the oospecies *M. pseudomamillare,* which means "similar to *M. mamillare*". Later, in their revision of megaloolithid eggs, Vianey-Liaud *et al*. (2003) propose to consider *M. pseudomamillare* a probably junior synonymous of *M. baghensis* (Khosla and Sahni, 1995). For more information and detail see Chapter 4.1.2.

This oospecies was also reported from Suterranya, Abeller, Orcau, Llavusta and Vicari sites in the Tremp basin (Moratalla, 1993; Vianey-Liaud and López-Martínez, 1997) and in Torrent de l'Esdavella in Vallcebre Syncline (Vila *et al*., 2011).

Chapter 5

NON-SAUROPOD EGGSHELLS FROM THE UPPER CRETACEOUS OF SOUTHERN PYRENEES

As it was pointed in previous chapters, *Megaloolithus* exhibits its hegemony about any other type of fossil eggs in the fossil record of the Pyrenean region, representing up to 90% of recovered material. This apparent low oological diversity, probably caused by sampling bias, not matches with the known dinosaur diversity in the Upper Cretaceous of Pyrenees. Nevertheless, as was pointed out by Vianey-Liaud and López-Martínez (1997), the oological diversity in Southern Pyrenees could be relatively higher. Based in eggshells fragments recovered from prospections works, they reported eight oospecies from Fontllonga-6 site (Àger Syncline, Lleida Province). Two of those were attributed to *Megaloolithus*, but five others were assigned to dinosauroid-prismatic morphotype and one to ornithoid-ratite morphotype. That preliminary work revealed an unexpected high diversity of fossil eggshells in the Upper Cretaceous deposits of North Spain, showing that more accurate fieldworks were needed to find other fossil eggshell types than *Megaloolithus*.

In this chapter it is listed and described non-megaloolithid oological material attributed to dinosaur, including the revision of *Cairanoolithus* material, the first evidence of spheroolithid eggshells in the Upper Cretaceous of Europe, and the description of a new prismatoolithid ootaxa.

5.1. CAIRANOOLITHID EGGS FROM THE UPPER CRETACEOUS OF SOUTHERN PYRENEES

5.1.1. Introduction

Cairanoolithid eggs are considered one of the most enigmatic types of dinosaur eggs ever found in Europe by its unique combination of structural characters (Vianey-Liaud *et al*, 1994). *Cairanoolithus* differs from its supposed sister ootaxon *Megaloolithus* for to exhibit a less developed external ornamental pattern; shell composed by fused columnar-shaped units; horizontal growth lines, and narrow and straight gas-exchange system canals.

Currently, three oospecies have been ascribed to *Cairanoolithus* oogenus: *C. dughii* (Vianey-Liaud *et al*., 1994) and *C. roussetensis* (Garcia and Vianey-Liaud, 2001a), both found in Provence area (France), and a new unnamed oospecies of ? *Cairanoolithus* from Rennes-le-Château site (Aude, France) (Cousin, 2002). The finding of these remains only in France, led to assume that *Cairanoolithus* must has been an endemic ootaxon from this region (Vianey-Liaud *et al*., 2003).

Herein, new remains attributed to *Cairanoolithus* found in Coll de Nargó Syncline (Lleida province, South Pyrenees) are described, reporting new structural characters for this type of dinosaur egg and a brief discussion about its parataxonomic implications and affinities.

5.1.2. Systematic Paleontology

VETEROVATA Vialov, 1972

Organization group: Dinosauroid

Structural morphotype: ? Discretispherulitic, ? Prolatospherulitic

Oofamily CAIRANOOLITHIDAE nov. oofam.

Diagnosis. – Dinosauroid-spherulitic basic type. Eggshell composed by nearly columnar-shape units frequently, but not completely, interlocking; growth lines mainly horizontals, sometime undulating, and parallel to eggshell surface; complex rimo-prolato- and tubocanaliculate pore system. Egg surface with a combination of disperse- sagentotuberculate ornamental patter. Differ from *Megaloolithidae* in the shape of shell units and ornamental pattern; and from *Ovaloolithidae* and *Spheroolithidae* in size and shape of eggs and pore system canal.

Type Oogenus. – *Cairanoolithus* Vianey-Liaud *et al*., 1994

Oogenus *Cairanoolithus* Vianey-Liaud, Mallan, Buscali, Montgelard 1994 (emend. Garcia and Vianey-Liaud, 2001)

Included Oospecies. – Three oospecies: *Cairanoolithus dughii* Vianey-Liaud *et al*., 1994; *Cairanoolithus roussetensis* Garcia and Vianey-Liaud, 2001a (= *Dughioolithus roussetensis*, Vianey-Liaud *et al*., 1994); ? *Cairanoolithus sensu* Cousin, 2002.

Time distribution. – Late Campanian and the beginning of the Maastrichtian (from C33n to C32n.1n).

Emended Diagnosis. – Modified from Garcia and Vianey-Liaud (2001a). Eggs sub-spherical in shape (15-20 cm); nearly columnar units not completely interlocking; growth lines horizontal in the interlocking shell units, slightly arched in the single units; dispersetuberculate and sagenotuberculate ornamental surface; narrow tubocanaliculate pore system, sometimes prolatocanaliculate and rimocanaliculate.

Oogenus *Cairanoolithus* Vianey-Liaud, Mallan, Buscail and Montgelard, 1994.

(emend. Garcia and Vianey-Liaud, 2001a)

Oospecies *Cairanoolithus aff. roussetensis*

(Fig. 19)

Material- 18 eggshells from "El Mirador" Level (IPS-59073) from Pinyes locality (Coll de Nargó Syncline, Alt Urgell). This material have been compared to several eggshells (IPS-59113) from Pinyes locality, 2 eggshells of *C. roussetensis* (IPS-58958) from Argelier (France), 4 eggshells of *C. dughii* (IPS-58956) from La Cairanne (Aix-en-Provence, France), 38 eggshells of *Spheroolithus* (IPS-58950 and IPS-58951) from "Egg Mountain" site (Montana, USA), and 1 eggshell of *Spheroolithus maiasauroides* (IPS-58954) from Inner Mongolia (China).

Description - One egg cluster composed by six sub-spherical eggs (17.5 x 16.8 cm in diameter) had been found in quartzite sandstones between Sallent and Pinyes sites. These eggs appear linearly arranged in two superimposed levels in lateral view, where some eggs are above the others (Fig. 19A). Two isolate eggs have been found in grey marls strata ("El Mirador" Level) in Pinyes nesting site. One egg appears partially broken and crashed, showing only the inner part of half egg and displaying an ovoid morphology (10 x 8 cm), while the other is nearly complete but crushed, and it is apparently ovoid in shape (13.4 x 8.9 cm). The shape of these eggs could be the result of Alpine tectonic process, which have taken place in this area during the end of the Cretaceous to the Eocene (Vila *et al*., 2010c).

The eggshells ranges from 1.11 to 1.64 mm in thickness with an average of 1.29 mm. Outer surface appears covered by fine undulate ridges and isolate rounded nodes. Ridges, which are 1.3 mm in wide, seem to be composed by fused fine nodes and without preferential orientation (Fig. 19C, D). Randomly scattered rounded nodes are 1.5 mm in diameter and 0.1 mm in thickness. They are separated from each other by flat areas. In radial thin section, eggshell units show a columnar shape (Fig. 19F, G) with straight edges. Frequently, these units are interlocked between adjacent ones in 2/3 parts of the total eggshell thickness; even sometimes it occurred in 90% of total thickness. The weight of shell units is about 0.47 mm, being the ratio h/w about 2.7. Growth lines are more or less horizontal and parallel (Fig. 19F), following the topography of the outer surface, and crossing the edges between adjacent fused units. However, in the lower part of shell units, growth lines are mainly arched. In the most basalt part of shell units there is a semispherical cavity left by the absence of organic core. Under polarized light, eggshell units show an irregular prismatic extinction pattern, as a result of a radial arrangement of prismatic wedges, which began to growth from the most basal part of the shell unit. (Fig. 19H). The study of these eggshells under SEM microscope reveals the presence of a radial-tabular ultra-structure (Fig. 19I) throughout the eggshell unit, confirming that eggshell units are composed by just one structural layer. This implies that eggshell belongs to dinosauroid-spherulitic basic type.

Also in radial thin section, pore canals have been observed and can be distinguished two different morphologies (Fig. 19F). The first one is characterized by to show narrow and straight canals, being wider in its upper part, and ranging from 71 to 130 µm in wide in its middle part, while oval-shaped pore openings in outs surface could be 0.17 mm in wide. This type of pore system seems to be a variation of angusticanaliculate pore systems, because canals display the same morphology but are wider than typical angusticanaliculate pore system defined by Mikhailov (1997). The second pore canal type is characterized by to show oblique and irregular pore canals. Some of these canals exhibit lacunas in its middle part, which are 107 µm in wide, while

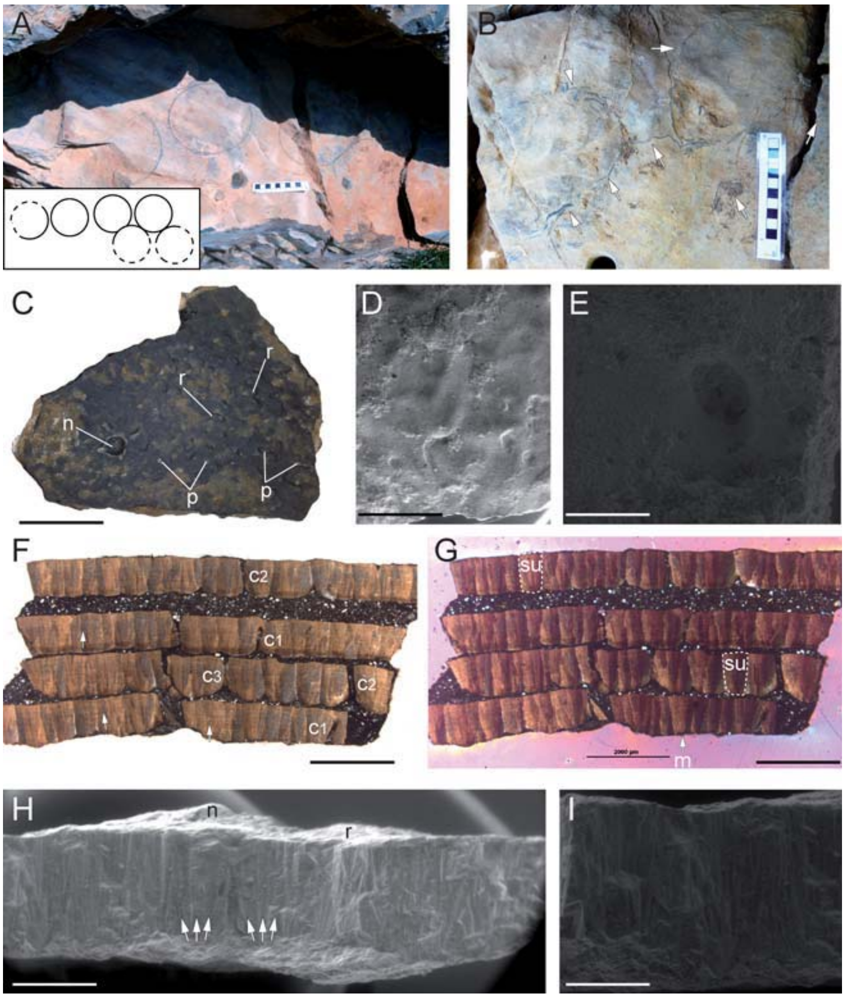

Figure 19. *Cairanoolithus aff. roussetensis* features. A) Lateral view section and schematic draw of cairanoolithid clutch. B) Detail of egg arrangement within clutch. Arrows show the position of eggshells C) Outer surface. D) Detail of the irregular ornamental ridges. E) Ovoid pore aperture in outer surface. F and G) radial thin section of eggshell. H and I) Eggshell under SEM. Arrows indicate the growth direction of calcite crystals. c: gas-exchange canal (c_1-sagenocanaliculate, c_2-narrow tubocanaliculate, c_3-rimocanaliculate) m: mamillae, n: nodes, p: pore apertures, r: ridges, su: shell unit. Scale bar: 10 cm (A, B); 5 cm (C); 3mm (F, H); 1mm (D, H); 500 µm (I); 150 µm (E).

the rest of canal ranges from 70 to 80 μm. All these characters are consistent with prolatocanaliculate pore system (Mikhailov, 1997), but this last pore type is rare.

Comparison. – Eggs and eggshells found in Sallent and Pinyes sites are undoubtedly attributed to *Cairanoolithus* oogenus, easily recognizable by its unique combination of structural characters. The three cairanoolithid oospecies described from France: *C. roussetensis* (Vianey-Liaud *et al.*, 1994), *C. dughii* (Garcia and Vianey-Liaud, 2001) and *Cairanoolithus* sp. (*sensu* Cousin, 2002). share the same macro- and microstructural characters and differ only in the egg dimensions; the thickness of eggshell, the pore diameter and the ornamental pattern. Eggs from Pinyes locality are similar to *C. roussetensis*, because both specimens show the same range of eggshell thickness and pore canals diameter. Also, both types exhibit similar ornamental pattern, consisting in isolated nodes and some fine ridges. However, cairanoolithid eggs from Pinyes locality show more pronounced ornamentation than *C. roussetensis*, more similar to cairanoolithid eggs from Rennes-le-Château site (Aude, France), and seems to exhibit a complex pore system canal (prolatocanaliculate + rimocanaliculate), while *C. roussetensis* has a simple system of respiratory canals (narrow tubocanaliculate). For all these reasons, here it is proposed to assign the oological material from "El Mirador" Level in Pinyes locality and Sallent site to *Cairanoolithus aff. roussetensis*.

5.1.3. Discussion

In 1994, Vianey-Liaud and colleges erected the *Cairanoolithus* oogenus, which was tentatively included in the oofamily Megaloolithidae (Mikhailov, 1996, 1997; Carpenter, 1999; and Garcia and Vianey-Liaud, 2001), but this affinity had been largely questioned (see Vianey-Liaud *et al*, 1994; Garcia, 1998 and Cousin, 2002). As it is showed above, there are many macro- and microstructural differences between megaloolithid and cairanoolithid eggs, such as the ornamental pattern, shell units shape, or pore system.

Megaloolithus is characterized for to exhibit a discretispherulitic morphotype, tubocanaliculate pore system and sculptured eggshell surface with compactitubercular ornamentation (Mikhailov, 1997).

Discretispherulitic morphotype implies that eggshell is composed by fan-shape shell units sharply separated from each other, rarely interlocked, and the growth lines are mainly concentric (*sensu* Mikhailov, 1997); while cairanoolithid eggshells are composed of columnar-shape shell units frequently interlocking with adjacent one, making it difficult to trace the edges between them, and the growth lines are mainly horizontals or slightly undulating and parallels to the eggshell surface.

Compactituberculate ornamentation implies that outer eggshell is covered mainly with dome-shaped tubercles, while *Cairanoolithus* is characterized by to show a combination of dispersituberculate (isolated nodes) and ramotuberculate (non oriented irregular ridges and soft nodes) ornamental patterns. Cousin (2002) also observed this character in cairanoolithid eggs from Rennes-le-Château site (Aude, France). He suggested that the ornamentation in *Cairanoolithus* could be a variation of sagentotubercular ornamental pattern (irregular ridges and nodes), typical for spheroolithid eggs; and in addition, gas-exchange canals in *Cairanoolithus* are more irregular and narrow than in *Megaloolithus*.

All these evidences suggest that *Cairanoolithus* oogenus cannot be referred to Megaloolithidae oofamily. In fact, Cousin (2002) considered *Cairanoolithus* an intermediate state between *Spheroolithus* and *Megaloolithus*. According to arguments given by Zelenitsky and Therrien (2008), higher-level parataxonomic groupings (basic types and morphotypes) are unnatural groupings making questionable their usefulness; many morphotypes are often synonymous with the oofamily, and proposing to abandon these terminologies. For these reasons, we propose to establish the new oofamily Cairanoolithidae nov. oofam.

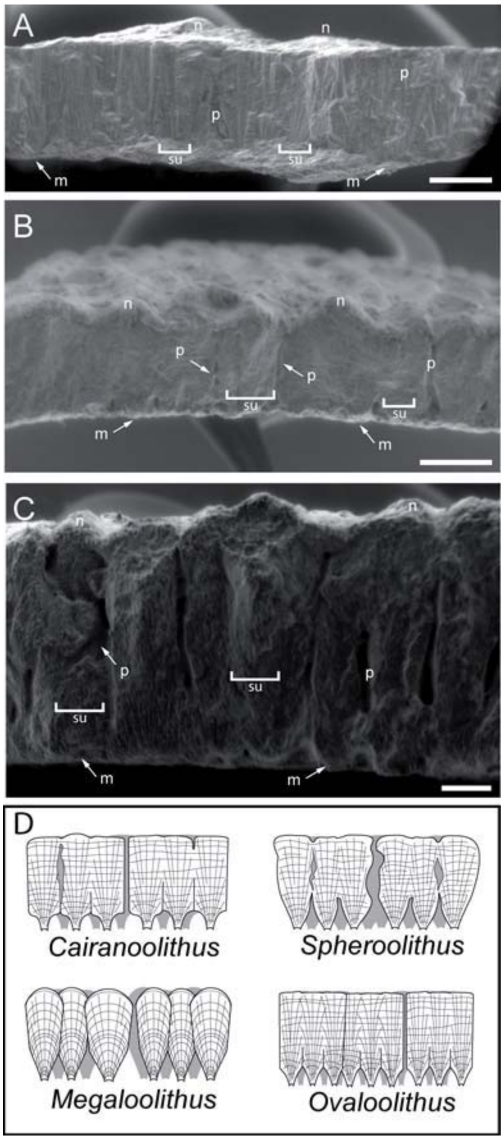

Figure 20. Comparison between eggshells of *Cairanoolithus* (A), *Spheroolithus* (B) and *Megaloolithus* (C). D) Diagrammatic comparison of the histostructure of dinosaur eggshells more related to *Cairanoolithus*. Scale bar: 0.5 mm.

If cairanoolithid eggs are compared to other dinosaur oofamilies, they shares a lot of structural characters with *Spheroolithidae* and *Ovaloolithidae*, such as columnar-shape shell units, frequently fused; undulating to horizontal growth lines and similar ornamental pattern and respiratory canal system. However, cairanoolithid eggs exhibit some differences with these oofamilies. First, spheroolithid and ovaloolithid eggs show typical sagentotuberculate ornamentation in outer eggshell, while in *Cairanoolithus* ornamental ridges are less developed and flatted areas are common between disperse nodes. Second, *Spheroolithus* exhibits a prolatocanalitulate pore system, while *Ovaloolithu*s and *Cairanoolithus* show a combination of rimo-prolato and narrow tubocanaliculate (? angusticanaliculate) pore system (Fig. 20).

Finally, these three oofamilies differ between them in the size and shape of egg. Spheroolithid eggs are slightly oval and rarely exceed 12 cm long and ovaloolithid eggs are mainly ellipsoidal with 9 cm of length, while cairanoolithid eggs are mainly subspherical and 16-18 cm in diameter.

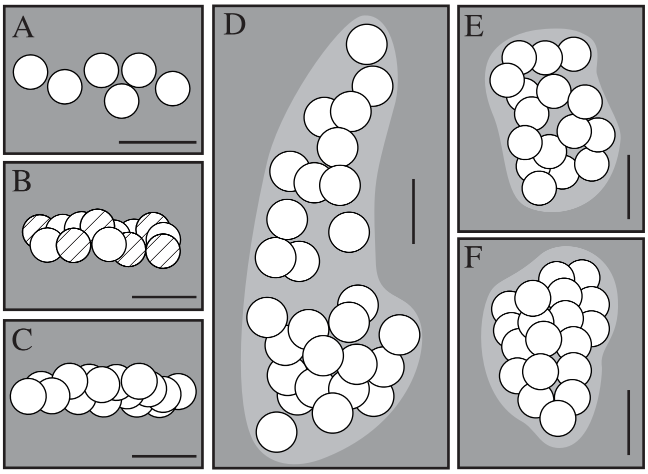

Figure 21. Comparison between clutches arrangement of different ootaxa in lateral view: A) Cairanoolithid eggs from Coll de Nargó Syncline, B) *Cairanoolithus* from Aix-en-Provence (France) and C) *Spheroolithus* of *Hypacrosaurus* sp.) from Montana (USA), and in upper view: D) *Megaloolihus* clutch from Pinyes site (modified from Vila et al., 2010), E) *Cairanoolithus* clutch from Aix-en-Provence (France) and F) *Spheroolithus* clutch of *Hypacrosaurus* sp. from Montana (USA).

Additionally, it is possible to do some consideration about the arrangement of eggs in the clutch found in Coll de Nargó Syncline. These cairanoolithid eggs showed a linear arrangement distributed in apparently two superposed layers in lateral view (Fig. 21A). This spatial distribution is also observed in the most complete cairanoolithid clutch known, which contain 27 eggs (Garcia, 1998; Cousin, 2002; see Fig. 21B), and in other clutches of *Cairanoolithus dughii* from southeastern France (Garcia, 1998). This type of lateral arrangement has been observed in other ootaxa, such as *Spheroolithus* (Fig. 21C), *Ovaloolithus* and *Dendroolithus* (Mikhailov *et al*., 1994b; Carpenter, 1999; Liang *et al*., 2009), and partially in *Megaloolithus* (Vila *et al*., 2010). However, in plant view, clutches of *Megaloolithus* exhibit an elongate arrangement of eggs (Vila *et al*, 2010; see Fig. 21D) while *Spheroolithus, Ovaloolithus* and *Dendroolithus* mainly show a close packing to loosely cluster pattern of egg clutches (Carpenter, 1999; see Fig. 21F), like it is observed in cairanoolithid clutches (Fig. 21E).

5.2. THE “THIN EGGSHELLS” FROM THE LATE CRETACEOUS IN SOUTHERN PYRENEES

5.2.1. Introduction

Historically, paleooological studies in the Late Cretaceous of South-Central Pyrenees have been focused in relatively thick eggshells. However, as it will be exposed below, Upper Cretaceous sediments from this area also contain an important record of fossil thin eggshells. This oological material has been traditionally poor studied and not well know.

The first study on fossil thin eggshells from South Pyrenees was conducted by Vianey-Liaud and López-Martínez (1997). They described four types of prismatoolithid eggshells and one oospecies of ornithoid-ratite from the Fontllonga-6 site (Àger Basin). Later, López-Martínez *et al.* (1999) distinguished six ornithoid eggshell types in Blasi-2 (Huesca Province, Southwestern Pyrenees), never described or figured. In fact, the “thinn eggshell” record is common in the Upper Cretaceous of Southern France (Vianey-Liaud and Crochet, 1993; Garcia, 2000); even it is as unknown as in Spain.

In this chapter, thin eggshells from different sites of the Late Cretaceous sediments from the South-Central Pyrenees will be described in detail.

5.2.2. Systematic Paleontology

VETEROVATA Vialov, 1974

Organisation group: Dinosauroid

Structural morphotype: Prolatospherulitic

Oofamily SPHEROOLITHIDAE Zhao, 1979

Oogenus *Spheroolithus* Zhao, 1979 (emended Mikhailov,1994)

Oospecies Spheroolithus oosp. nov.

(Fig. 22)

Material — 112 eggshell fragments (ISP-58973) from Porri-6 site (Pont d’Orrit, Tremp Basin).

Description — Most of eggshell fragments recovered from Porri-6 site measures up to 5 mm^2. Its outer surface exhibits linear and bifurcating ridges, characteristic of sagenotuberculate ornamentation (Fig. 22A). These ridges are about 180 μm in width. Pores on the eggshell surface typically occur between the ridges

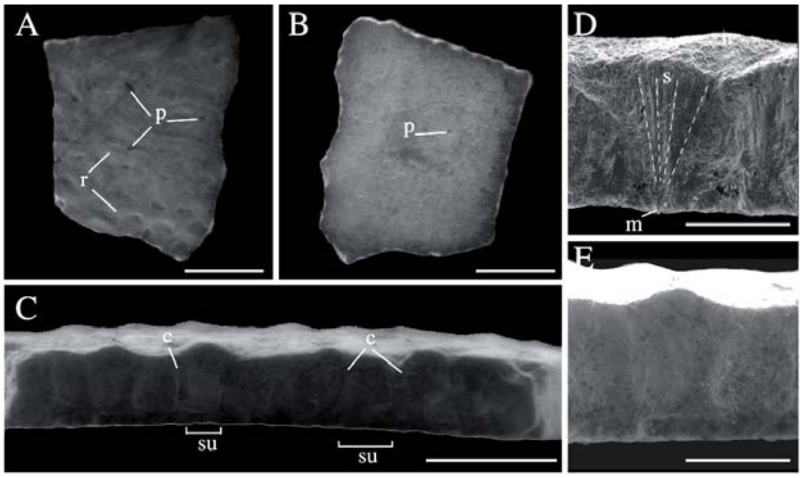

Figure 22. *Spheroolithus* nov. oosp. (ISP-58973). A) Outer surface of the eggshell showing the ornamental pattern and pore apertures. B) Inner part of the shell exhibiting relatively wide mamillae and the situation of pore canals. C) Shell units appear nearly interlocked and pores placed between them in radial view. D-E) Detail of a shell units and its relation with ornamental nodes. c-canal pore; m- mamillae; n-nodes; p- pore aperture; r-ridges; s-spherulites; su- shell unit. Scale bar: 2 mm (A, B, C) and 1 mm (D, E).

and vary from round, to sub-round, to narrow slits (Fig. 22A). In fact, it could be distinguished two types of pores apertures: a big elliptical aperture (0.3 x 0.64 mm) and a small rounded one (about 0.1 mm in diameter), which sometimes appear paired. These two types of pores apertures in the outer surface could be related with variations in a prolatocanaliculate pore system, where elongate pore openings could belong to foveocanaliculate canals while small ones could be attributed to lagenocanaliculate canals (Mikhailov, 1997; Carpenter, 1999). Apparently, small apertures are more abundant than bigger, being the total density of pore about 48 pores per 100 mm^2. The eggshell thickness varies from 1.04 to 1.11 mm, with an average value of 1.07 mm (Fig. 22C). A preserved mammillary core measures 55 µm in diameter. Distances between the nuclei vary from closely spaced to widely separate; the latter typically occur when shell units are separated by a pore (Fig. 26B).

In radial views calcite spherulites emanate from nucleation sites at the inner shell surface and radiate outwards, forming narrow wedges, which comprise the shell units (Fig. 22D). Pore canals appear between shell units, which vary in width (50 - 100 µm) along their length, as correspond to prolatocanaliculate pore system (Fig. 22C). Fan-shaped shell units appear partially fused, being difficult to distinguish the edge between them. The growth line lamination is undulating, sometimes following the topography of outer eggshell surface (Fig. 22E).

Comparisons and Discussion — Characters described above are consistent with prolatospherulitic morphotype, which is represented by only one oological group, *Spheroolithus*. Currently, *Spheroolithus* is represented by ten formally recognized oospecies, which are distributed from Canada, USA, China, Mongolia and South Korea. Eggshell from Porri-6 site differs from the Chinese oospecies *Spheroolithus irenensis* (Zhao and Jiang, 1974), *S. tenuicorticus* (Mikhailov, 1994b), *S. zhangtoucaoensis* (Fang *et al.,* 2003) and *S. jincunensis* (Fang *et al.*, 2005) in the outer surface ornamentation, being those Asian oospecies smooth or slightly rough. *Spheroolithus chiangchiungtingenesis* (Zhao and Jiang, 1974) and *S. megadermus* (Young,

1959) exhibit considerable thick eggshell (2.7 mm and 5.7 mm, respectively), and their outer surfaces are sculptured with irregular nodes, while ISP-58973 is 1.07 mm in thickness and it shows a sagenotuberculate ornamentation. The Mongolian oospecies *S. maiasauroides* (Mikhailov, 1994b) exhibits sagenotuberculate ornamentation, but it is thicker (1.2-1.5 mm) than Catalan specimen. *Spheroolithus albertensis* (Zelenitsky and Hills, 1997) from Canada is as thick as studied material, but Canadian oospecies shows a finer and more variable ornamentation than the eggshell from Porri-6 site. Jackson and Varricchio (2010) described the oospecies *S. choteauensis* from the lowermost part of the Two Medicine Formation of western Montana (USA). This oospecies is somewhat thinner (0.66-0.94 mm in thickness) than spheroolithid eggshell from Southern Pyrenees and the American ootaxon exhibits different ornamental pattern.

Finally, eggshells from Porri-6 site, which represent the firt evidence of this type of dinosaur eggshells in Europe, are similar to spheroolithid eggshells attributed to *Maiasauran peeblesorum* from the Two Medicine Formation of Montana (Horner and Makela, 1979). Those eggs and eggshells were described by Hirsch and Quinn (1990), but never were parataxonomically classified. Both ootaxa have the same sagenotuberculate ornamental patter in outer surface of the shell and they also show similar rang of eggshell thickness (*Maiasaura* is 1.0-1.2 mm and ISP-58973 is 1.04-1.11 mm in thickness). However, additional measures made in eggshells of *M. peeblesorum* (IPS-58950, IPS-58951) revel that many of these eggshells exceed 1.4 mm in thickness, being the North American ootaxon thicker than Catalan specimen. Both oospecies also exhibit similar pore canals apertures in the outer surface of eggshells, even showing the same shape and dimensions. However, eggshells of *Maiasauran peeblesorum* do not show a second type of pore openings, the big elliptical ones, as occur in spheroolithid eggshell from Porri-6 site.

All these characters suggests that *Spheroolithiu* from Porrit-6 site could represent a new ootaxon and the first *Spheroolithus* oospecies from the Upper Cretaceous of Europe.

Structural morphotype: Prismatic

Oofamily PRISMATOOLITHIDAE Hirsch, 1994

Oogenus Prismatoolithus Zhao and Li, 1993 (*sensu* Zelenitsky and Hills, 1996)

Oospecies *Prismatoolithus* nov. oosp.

(Fig. 23, Fig. 24A)

Material — more than 150 eggshell fragments (?IPS-58961, IPS-58962, IPS-58972, IPS-58976, IPS-58978, IPS-58983, IPS-58985, IPS-58990, IPS-59116) and one thin section (1A07). This oological material comes from different sites, such as La Massana outcrop (Àger Syncline), L'Espinau, Barranc de la Boiga, Serrat del Rostiar, Basturs-Poble, Molí del Baró, and Camí del Soldat sites (Tremp basin).

Description — Eggshells range between 0.25-0.53 mm in thickness, with an average value of 0.39. Outer surface is generally smooth or slightly rough, but some fragments show a peculiar ornamental pattern (Fig. 23A). This ornamentation consists in some small flat pits, irregularly scattered on the outer surface. Apparently, pits tend to be grouped in clusters of 5 to 10 tubercles. This arrangement of nodes is present in some eggshells from L'Espinau outcrop (IPS-58972) as lineartuberculate ornamentation. Pore apertures are scattered in the smooth surface, showing an oval shape (Fig. 23A). Frequently, the inner surface appears weathered, and eisospherulites are quite eroded (Fig. 23B). When they are present, spherulites are relatively width (0.2 mm) and closely packet.

In radial view, shell units exhibit a columnar shape with two distinguish parts (Fig. 23C, Fig. 24A): the upper columnar layer and the lower mammillary layer, according to prismatic morphotype (Mikhailov, 1997). The columnar layer is composed of vertical irregular prisms, while mammillary layer is formed of crystalline wedges. The SEM observation reveals the gradual transition between wedges and columns (Fig. 23D, E), being the mammillary layer 1:3-1:4 of the whole thickness (Fig. 23D). Horizontal to undulating growth lines are clear in the columns than in the wedges. The rare pore canals are straight and about 50 µm in diameter, which is typical angusticanaliculate pore system (Fig. 23C).

Comparison and Discussion — The columnar shape of shell units, the gradual transition between mammillary and columnar layers and the relatively smooth outer surface of the eggshells are unequivocal characters to attribute studied material to *Prismatoolithius* oogenus. This type of prismatic eggshells is present in the Upper Cretaceous from USA,

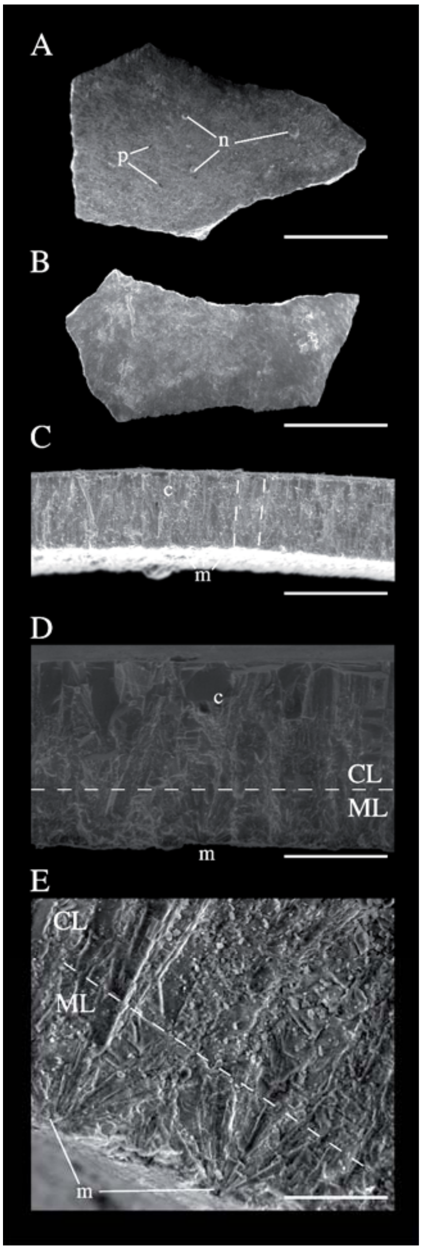

Figure 23. *Prismatoolithus* nov. oosp A) Outer surface of the eggshell showing the ornamental pattern and pore apertures. B) Inner part of the shell frequently appears weathered. C) Prismatic-shaped shell units appear nearly interlocked and pore canals are placed between them in radial view. D) Eggshell shows gradual transition between continuous layer and mamillary layer. E) Detail of the transition between continuous and mamillary layers. c-canal pore; CL-continuous layer; m- mamillae; ML- mamillary layer; n-nodes; p- pore aperture. Scale bar: 1 mm (A, B), 500 µm (C), 250 µm (D) and 100 µm (E).

Canada, Mexico, France, Spain, Russia and China, and includes nine oospecies. All prismatoolithid oospecies, excluding *P. hirschi* from Montana (Jackson and Varricchio, 2010), exhibit a gradual transition between mammillary and columnar layer as occurs in prismatoolithid eggshells from South Pyrenees. The studied material is thinner than *P. matellensis* (Vianey-Liaud and Crochet, 1993), *P. levis* (Zelenitsky and Hills, 1996), *P. jenseni* (Bray, 1999) and *P. hukouensis* (Zhao, 2000). *Prismatoolithus caboti* from France (Garcia *et al.*, 2000) is somewhat thicker (0.5-0.6 mm) than studied eggshells (0.25-0.53 mm). Finally, *Prismatoolithus tenuis* from the Campano-Maastrichtian of France and Spain (Vianey-Liaud and Crochet, 1993; Vianey-Liaud and López-Martínez, 1997) shows similar thickness range (0.3-0.6 mm) than those of Àger and Tremp basins.

In addition, the *Prismatoolithus* oospecies from Catalonia exhibits a mainly smooth outer surface but showing a peculiar ornamentation composed of small and irregular flat pits, that it is also displayed by *P. tenuis.* But this new ootaxon differ from the French one in the cl/ml ratio, being lesser in Catalan oospecies (see more details in Table 12).

A unique specimen of a new unnamed *Prismatoolithus* described by Vianey-Liaud and López-Martínez (1997) was reported from Fontllonga-6 site. That specimen exhibits the same microstructural characters than those observed in eggshells described above, such as shell thickness, pore aperture size and shape, cl/ml ration and ornamental patter, and even the irregular prismatic zone. All evidences suggest that the new oological material from Southern Pyrenees belong to a new oospecies of *Prismatoolithus*, which is also present in Fontllonga-6 site.

Oospecies *Prismatoolithus* cf. *levis* Zelenitsky and Hills, 1996

(Fig. 24B)

Material — A single eggshell fragments in radial thin section (1B01) from La Massana outcrop (Fontllonga section, Àger Syncline) was recovered during sampling of charophytes (Villalba-Breva, per. com.).

Description — The unique specimen from La Massana outcrop shows a prismatic morphotype and it is 0.85 mm-thick. The outer surface is apparently smooth but it is somewhat eroded, as occur in the inner shell surface. In radial view, shell units are traceable through whole the eggshell thickness, and the ratio between structural layers is about 1:7. Any respiratory canal has been observed in radial section.

Comparison and Discussion — It is difficult to attribute with certainty this specimen with only one shell fragment. However, the shell thickness and the cl/ml ratio exhibited by 1B01 are consistent with *Prismatoolithus levis* from the Campanian of North America (Zelenitsky and Hills, 1996) (see Table 12). Both specimens exhibit narrow prismatic shell units easily distinguish in radial section. *P. levis* show a smooth egg surface, but this condition is no insurable in 1B01, because it could be reworked or weathered. One of the diagnostic characters of *P. levis* is the paring of the pores in the outer surface. Unfortunately, this character has not been observed in 1B01. Anyway, both ootaxa look like very similar and we, in absence of further material, tentatively assign the eggshell fragment from La Massana outcrop to *Prismatoolithus cf. levis*

Prismatoolithus sp. indet.

(FIG. 24C)

Material — Five eggshell fragments (1A01, 1A04, 1A06, 7B03, 7B05) from La Massana outcrop (Fontllonga Section, Àger Syncline).

Description — Only five shell fragments have been found in La Massana outcrop. These very thin eggshells range between 0.11-0.16 mm in thickness, and exhibit clearly a prismatic morphotype. Their outer surface is generally smooth but some specimens seem to show irregular undulating surface (e.g. 1A01). In radial section, shell units are well traceable through whole the eggshell thickness, which are composed of mammillary layer and continuous layer. The transition among both layers is made gradually, being the ratio between them about 1:2. Any pore canal has been observed.

Comparison and Discussion — Due to prismatic morphotype and more or less smooth surface exhibited by eggshells from the Fontllonga section, those eggshells could be referred to *Prismatoolithius* oogenus. The thickness ratio between structural layers (cl/ml) exhibited in shell fragment from La Massana outcrop is similar to those *Montanoolithus strongorum* (Zelenitsky and Therrien, 2008) and *Prismatoolithus hirschi (*Jackson *et al*., 2010), but eggshells from La Massana differ from the first in outer surface ornamentation (see Table 12) and from the second in the gradual transition observed between structural layers. Also, prismatoolithids eggshells described here are thinner than both previous oospecies. Indeed, any known *Prismatoolithus* oospecies

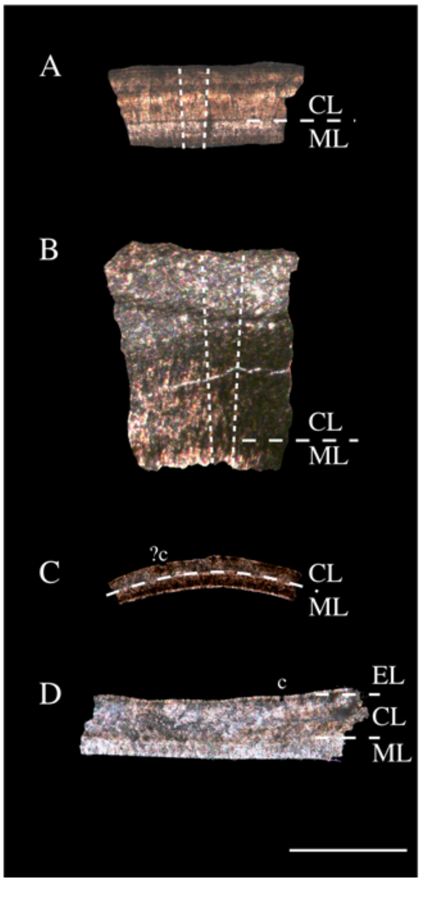

Figure 24. *Prismaotlithus* and ornithoid-ratite eggshells from La Massana outcrop showing the CL/ML ratio and the prismatic shape of shell units. A) *Prismatoolithus* nov. oosp. (1A07), B) *Prismatoolithus cf. levis* (1B01), C) *Prismatoolithus* sp. indet. (1A06), and D) cf. *Ageroolithus* (1B04). c-pore canal; CL- continuous layer; EL-external layer; ML- mamillary layer. Scale bar: 500 µm.

shows similar thickness like eggshells here reported, being a half of thickness of the thinnest prismatoolithid oospecies, *Prismatoolithus tenuis*. Thus, all evidences suggest that these eggshells could represent a new ootaxon of *Prismatoolithus*, but further material is needed to confirm this hypothesis.

Organisation group: ? Lizard

Structural morphotype: ? Geckoid

Oofamily ? GECKOOLITHIDAE Hirsch, 1996

Oogenus Pseudogeckoolithus Vianey-Liaud and López-Martínez, 1997

Pseudogeckoolithus sp.

(Fig. 25)

Material — More than 1000 eggshell fragments (IPS-58970, IPS-58971, IPS-58977, IPS-58980, IPS-58986, IPS-58989, IPS-58993) coming from different sites: Molí del Baró, Serrat del Pelleu, Serrat del Rostiar, Camí del Soldat and L'Espinau (Tremp basin).

Description — Eggshells are very thin, ranging from 0.21-0.35 mm, including ornamentation; and 0.15-0.22 mm, without ornamentation. The outer surface is covered by small irregular and scattered knobs or nodes of 50-200 µm in diameter, like in the dispersituberculate ornamental type (Fig. 25A-C). Pore canal apertures are located at the top of these nodes (Fig. 25E) and less frequently in flat area between nodes. Nodes are not really abundant, approx. 6-7 nodes/mm^2, and their distribution is also irregular (Fig. 25A-C). Pore apertures are circular in shape and range from 30 µm to 50 µm in diameter.

In radial section, eggshell exhibit a single structural-layers of not well distinguish prismatic-shape shell units. Under SEM, shell units exhibit irregular prismatic crystals (Fig. 25D), which also show spongy squamatic texture (Fig. 25F). Horizontal to undulating growth lines appear in the median part of the thin sections. The inner surface lacks mammillae knobs or organic cores, but is covered for irregular granules of calcite. No signs of weathered or alteration are appreciated in the inner part of shells, suggesting that these eggshells never had mammillae. Really narrow and straight pore canals are visible, ranging from 30 µm to 50 µm in wide, as corresponds to the angusticanaliculate pore system type.

Comparison and Discussion — Apparently, eggshells described above exhibit prismatic structure, but they area also similar to geckonoid morphotype. In fact, the dispersituberculate ornamentation with pore apertures located in the top of nodes is a unique character in the fossil record, being exclusive of the oogenus *Pseudogeckoolithus*, which includes two oospecies, *P. nodosus* (Vianey-Liaud and López-Martínez, 1997) and *P. triboulensis* (Vianey-Liaud and Garcia, 2004). Both oospecies have thin eggshells (about 0.28 mm in

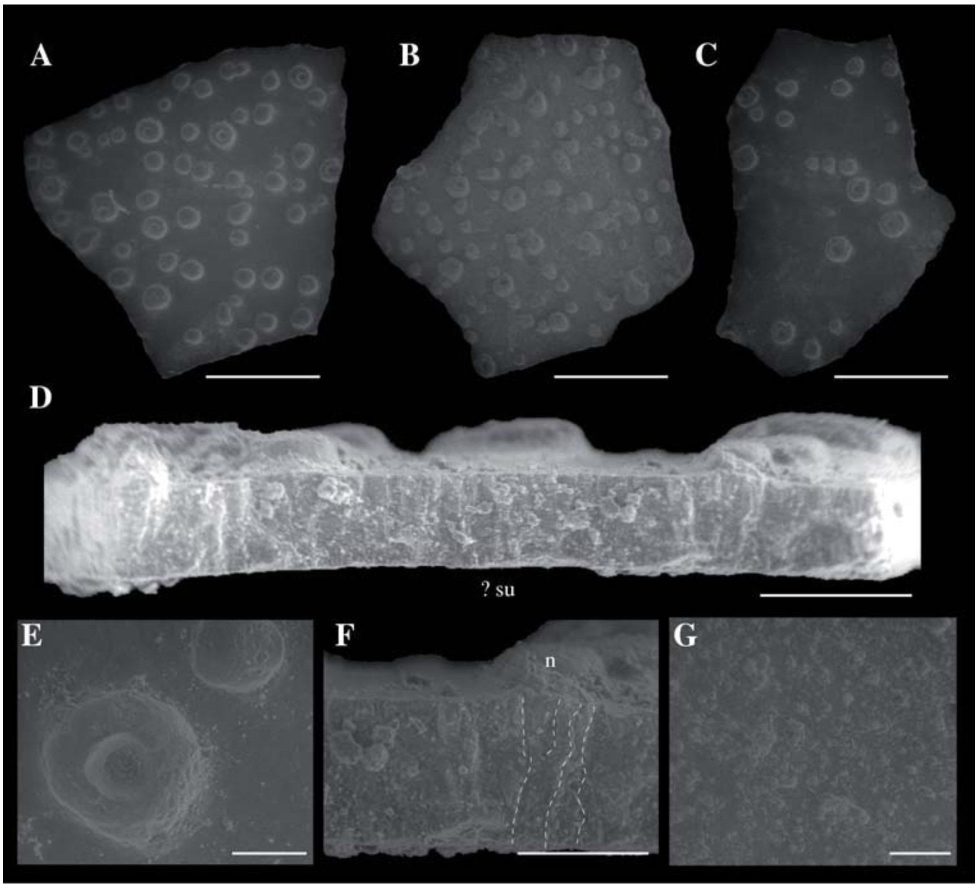

Figure 25. *Pseudogeckoolithus* sp. A, B, C) Variability of the external ornamental pattern in the outer surface of the shell. D) Radial view of shell structure, where is noted the difficulty to distinguish shell units. E) Detail of the pore aperture located at the top of nodes. F) Detail in a radial view showing the irregular shape of the fused shell units. G) Magnification of the inner part of the shell exhibit the absence of mamillae and the presence of irregular granules. Scale bar: 1 mm (A, B, C); 500 µm (D); 200 µm (F); 100 µm (E, G).

thickness) and small pore openings (30 µm in diameter) and both characters are present in "pseudogeckoolithid" eggshells from South Pyrenees.

But here, the main problem with specimens from the Late Cretaceous of Southern Pyrenees is related to the absence of mammillae in the inner part of the shell. The revision of *Pseudogeckoolithus* ootaxa reveals a series of possible misinterpretations of microstructural characters. First, and one of most important problems, is that both pseudogeckoolithid oospecies had been created in base of very few samples, while here we have been examined more than 10000 eggshells. Second, according to Vianey-Liaud and López-Martínez (1997), *Pseudogeckoolithus nodosus* could exhibit a very thin mammillary layer, being only the 1/10 to 1/8 of the whole thickness. But this character in not present in any of eggshells from Fontllonga-6 site, and consequently eggshells are composed of a single structural layer of irregular prisms (see Vianey-Liaud and López-Martínez, 1997; fig.7.3). In the case of *Pseudogeckoolithus triboulensis*, Vianey-Liaud and Garcia (2004) interpreted that mammillary layer was as thick as prismatic layer, but this observation was made based on a re-crystallized eggshell (Vianey-Liaud and Garcia, 2004; Plate 6.a). On the other hand, other specimens of *P. triboulensis* do not show mammillary structures (Vianey-Liaud and Garcia, 2004; Plate 6.b-d), revealing that eggshell is only composed of irregular prismatic units. If our interpretations are right, it would means that *Pseudogeckoolithus* is not a dinosauroid-prismatic ootaxon, as was firstly interpreted (Vianey-Liaud and López-Martínez, 1997).

These results suggest a different origin for pseudogeckoolithid eggs. Hirsch (1996) describes the eggshell of extant gecko as composed of interlocking compact layer of columnar units, which show rounded structures in the inner part of the shell. Mikhailov (1997) also observed that eggs of geckos lack organic cores or basal plate groups, but they show peculiar spherical organic bodies attached at the base of shell units. Similar observations have been made in eggshells of extant (Schleich and Kästle, 1998) and extinct (Kohring, 1991; Hirsch, 1996; Mikhailov, 1997; Shukla and Srivastava, 2008) lizard. Pseudogeckoolithid eggshells reported here from South Pyrenees exhibit similar microstructural characters described above for extant eggs of lizard. For those reasons it is proposed that *Pseudogeckoolithus* could be related with some group of Mesozoic lizard.

Structural morphotype Ornithoid-ratite

oofamily *Incertae sedis*

Oogenus cf. Ageroolithus Vianey-Liaud and López-Martínez, 1997

Oospecies indet.

(Fig. 24D)

Material — two shell fragments in radial thin section (1B01, 1B04) from La Massana outcrop (Fontllonga Section, Àger Syncline).

Description — Eggshell fragments range between 0.278-0.288 mm in thickness. Outer surface is mainly smooth but with some undulation. In radial section, shell units show three structural layer, mammillary layer, continuous layer and external zone, exhibiting clearly a ornithoid-ratite morphotype. Continuous layer is twice the thick of the mammillary one, which are limited by a sharp contact. Shell units are only visible in the mammillary layer, while they are completely fused in the continuous one. In this last structural layer, growth lines appear mainly horizontal. External zone is composed of blocky calcite crystals, which is 20 μm thick. One straight pore canal has been observed in 1B04 (Fig. 24D), which is 19-20 μm in wide, corresponding to angusticanaliculate pore system.

Comparison and Discussion — These thin ornithoid-ratite eggshells share some structural characters with *Ageroolithus fontllongensis.* This fossil eggshell was previously reported in the same Fontllonga section (Vianey-Liaud and López-Martínez, 1997) and in Vitrolles-Couperigne outcrops in Southeastern France (Garcia, 2000), but it is only known by very scarce shell fragments. Specimen found in La Massana outcrop is as thick as *Ageroolithus*, even the thickness ratio between mammillary layer and continuous layer are similar in both ootaxa (Tables 12). Also, in both ootaxa outer surface of eggshell is mainly smooth, showing small pores (20 μm in wide) and narrow and straight respiratory canals.

The main difference between eggshells from La Massana site and *Ageroolithus* is the presence of a third structural layer or external zone. Vianey-Liaud and López-Martínez (1997) noted that some specimens from Fontllonga-6 site exhibited a thin calcitic recrystallized outer layer, which was attributed to diagenetical process (see Vianey-Liaud and López-Martínez, 1997, Fig. 10.2). However, the thickness of that "recrystallized layer" is as thick as external layer reported in new specimens from La Massana outcrop (20 µm). Thus, it would means that *Ageroolithus* is composed of three structural layers and it would be closely related with birds, but without more material these appreciations cannot be corroborated. Therefore, ornithoid-ratite eggshells from La Massana outcrop are tentatively attributed to *cf. Ageroolithus*.

MORPHOTYPE	OOFAMILY	TAXON/OOTAXON	SHELL THICKNESS (mm)	CL/ML RATIO	ORNAMENTATION
Dinosauroid-prismatic	Prismatoolithidae	*P. matellensis* Vianey-Liaud and Crochet, 1993	1.06-1.22	1:10	smooth
		P. tenuis Vianey-Liaud and Crochet, 1993	0.24-0.6	1:6	dispersituberculate
		P. caboti Garcia, 2000	0.5-0.6	1:8-1:10	dispersituberculate
		Prismatoolithus nov. sp., aff. P. matellensis Vianey-Liaud and López-Martínez, 1997	1	-	smooth
		P. gebiensis Zhao and Li, 1993	0.7-0.9	-	smooth
		P. levis Zelenitsky and Hills, 1996	0.7-1	1:6-1:8	smooth
		P. hirschi Jackson et al., 2010	0.5-0.56	1:2-1:2.5	smooth
	? Prismatoolithidae	*nov. gen et sp., sensus* Vianey-Liaud and López-Martínez, 1997	0.5	1:4	mainly smooth
	Montanoolithidae	*Montanoolithus strongorum* Zelenitsky and Therrien, 2008	0.70–0.85	1:2	anastomosing
	Incertae sedis	*Pseudogeckoolithus nodosus* Vianey-Liaud and López-Martínez, 1997	0.24-0.32	1:8-1:10	dispersituberculate
Ornithoid-ratite	Elongatoolithidae	*Deinonychus antirrhopus* egg Grellet-Tinner and Makovicky 2006	0.44-0.6	1:2	anastomosing
		Oviraptoridae egg Norell et al. 1994	0.50–0.954	1:34-1:2.55	linear ridges and nodes
	Incertae sedis	*Ageroolithus fontllonguensis* Vianey-Liaud and López-Martínez, 1997	0.25-0.36	1:2-1.5:2	smooth

MORPHOTYPE	OOFAMILY	OOTAXON	SHELL THICKNESS (mm)	CL/ML RATIO	ORNAMENTATION
Dinosauroid-prismatic	Prismatoolithidae	*Prismatoolithus nov. sp.*	0.39	1:3-1:4	mainly smooth
	Prismatoolithidae	*Prismatoolithus cf. levis*	0.854	1:7	? smooth
	Prismatoolithidae	*Prismatoolithus sp. indet.*	0.115-0.164	1:2	smooth
Ornithoid-ratite	Incertae sedis	*cf. Ageroolithus fontllongensis*	0.278	1:2	? undulating

Table 12. (Upper table) List of prismatic and ornithoid-ratites oospecies known worldwide compared with (Lower table) the list of prismatic and ornithoid-ratites oospecies from La Massana outcrop.

Chapter 6

PHYLOGENETYC ANALYSIS ON DINOSAUR FOSSIL EGGS

In the last decade, many authors proposed to apply phylogenetic analysis to evaluate the relationships between different types of fossil eggs (Grellet-Tinner, 2000; Varricchio and Jackson, 2004; Zelenitsky and Currie, 2004; Garcia *et al*., 2006; Grellet-Tinner and Makovicky, 2006; Zelenitsky and Therrien, 2008; Jin *et al*., 2010). Similar works were made with eggs of extant animals, such as paleognatha birds (Grellet-Tinner, 2000, 2006) and turtles (Winkler, 2006), showing that phylogenetical analysis made with eggs and eggshells have taxonomical signal. In these studies many structural characters of egg and eggshell are considered and some others, concerning characters of the nest and the relationship between the egg and the adult.

6.1. Phylogenetical relationship between megaloolithid oospecies

As was showed in Chapter 4.1.2, it is possible to distinguish three major structural groups in *Megaloolithus* oogenus. Some structural features are shared by all oospecies, and others are only present in a specific group. Here, we attempt to test if it is possible to establish relationships between different megaloolithid oospecies and other ootaxa.

Phylogenetic analysis was conducted using the brunch-and-bound search algorithm of PAUP 4.0 software (Swofford, 1998) on 10 *Megaloolithus* oospecies, *Spheroolithus problematica nov. com*. and 13 additional ootaxa. Many taxa and ootaxa are coded according to Varricchio and Jackson (2004), Garcia (2006) and Jin *et al*. (2010). One additional ootaxa has been codified here according to literature description and own observations: *Faveoloolithus* (Mikhailov, 1997, Casadío *et al*., 2002; Salgado *et al*., 2007; Salgado *et al*., 2009). We decided to code *Faveoloolithus* oogenus because it is considered to be a sauropod fossil egg, as *Megaloolithus*. The coding of megaloolithid oospecies has been made based on literature descriptions, personal observations and previously mentioned considerations.

The data matrix includes 22 characters (see Appendix II), 20 of which are referred to micro- and macrostructural characters of eggs and eggshells (character 1 to 20), one character with egg size/adult size ratio (character 21), and the other corresponds to the arrangement of egg within the clutch (character 22). All characters, excluding characters 20, 21 and 22, have been taken from Varricchio and Jackson (2004) and Jin *et al*. (2010). However, some character stats have been modified respect those previous works.

Jin *et al*. (2010) proposed to code as unknown character state (?) the composition of mammillary layer in *Maiasaura* and titanosaur eggs (character 4), but Varricchio and Jackson (2004) coded them as crystalline composition (character state 0). We agree with this last interpretation, because only crocodiles show mammillary layers formed by organic and crystalline material (Ferguson, 1985; Mikhailov, 1997). *Faveoloolithus* shares the same character state with *Maiasaura* (*Spheroolithus*) and titanosaur (*Megaloolithus*) egg. In Varricchio and Jackson (2004) and in Jin *et al*. (2010), the form of crystals radiating from the base of the shell units (character 5) is coded as: truncated, irregular or blocky. However, we prefer to refer them as: acicular, wedge-like and bladed-shape or tabular, because these terms are more common in the literature (Hirsch, 1996; Mikhailov, 1997; Bray and Hirsch, 1998; Garcia *et al*., 2006; Grellet-Tinner and Makovicky, 2006; Zelenitsky and Therrien, 2008; among others).

Similar considerations are applied for character 16. In previous works, the ornamentation of the outer surface of the eggshells was coded as present or absent. Here, this character is modified to specify the ornamental pattern type, such as smooth, with ridges, combining ridges and nodes or nodular (see characters 16).

Furthermore, we added three new codified structural characters (characters 17, 18, 19). Character 17 is referred to the fusion between adjacent shell units. Basically, it is possible to distinguish three states of fusion in shell units:

1) Without fusion, that is the primitive state in amniotes eggshell (Deeming and Unwin, 2004) and it is exhibit by eggshells of extant and fossil turtles, lizards, snakes and crocodiles. This character state is shared by some dinosaur eggs, such as the most of the oospecies of *Megaloolithus* and *Faveoloolithus* (Mikhailov, 1997; Carpenter, 1999).

2) Other dinosaur eggshells show a partial fusion between neighboring shell units, which frequently take place in the upper half of the shell units. This character seems to be common in eggshells with dinosaur-spherulitic basic type, such as *Spheroolithus* and some *Megaloolithus* oospecies (Mikhailov, 1997, Carpenter 1999).

3) Shell units can be completely interlocked, difficulting to dishing between individual units, which is the

typical state of extant birds, shared by the most of theropod eggs, prismatic basic types (*Preprismatoolithus* and *Prismatoolithus*) and ornithoid basic type (*Elongatoolithus, Macroelongatoolithus* or *Laevisoolithus*) (Mikhailov, 1997).

Character 18 tears about the shape of shell units. Non-specific terminology has been reported to describe the shape of shell units. Mikhailov (1997) established two main morphologies: Fan-shape and prismatic/columnar-shape. Khosla and Sahni (1995) used the term cilindric-shape to describe some Indian eggshells. Here, we propose to establish four categories for describing the shape of shell units. The primitive character, as occurs in turtles and crocodiles shell, is characterized for short-fan-shaped shell units (state 0), which is also exhibit in *M. jabalpurensis* and *M. mamillare.* Others *Megaloolithus*, such as *M. cylindricus*, *M. siruguei*, *M. mohabeyi*, *M. khempurensis*, M. *maghrebiensis*, and *Faveoloolithus* are composed for slender and elongate fan-shape shell units (state 1). Irregular fan-shape units (state 2) are present in many types of dinosaur eggs as noted in Mikhailov (1991, 1997). This morphology is not only present in *Spheroolithus* and *S. problematica* but also in some *Megaloolithus* (e.g. *M. aureliensis, M. baghensis* and *M. dholiyaensis*). Theropod and avian eggshells show prismatic-shaped (state 3) shell units (Mikhailov, 1997).

Finally, we propose to include character 19, related with the thickness of the shell, which is very variable within Megaloolithidae oofamily. In this group of fossil eggs shells can be thinner than 1 mm (state 0), like *M. aureliensis*; ranging from 1 to 2 mm (state 1), as occurs in *M. mamillare* or *M. baghensis*; up to 2 mm (state 2), such as *M. siruguei*; and thicker than 3 mm (state 3) as observed in *Faveoloolithus.*

6.1.1. Results of the phylogenetic analysis

The phylogenetic analysis produced 432 maximum parsimony tree (tree length= 46, CI= 0.78, HI= 0.22, excluding one uninformative character (character 10); and RI=0.89). The strict consensus tree can distinguish between non-archosaurian, represented by a triple polytomy of turtles, and archosaurian eggshells, including crocodiles, dinosaurs and birds (Fig. 26A). The phylogenetic position of each of these groups is not well resolved within Archosauria clade (node 1), but it is possible to observe, at least, four structural groups of eggshell. First, the order Crocodilia (node 2), composed of *Alligator* and *Crocodylus* eggshells, appears well supported in this tree. Megaloolithid oospecies of MG2 group and *M. dholiyaensis* are included in the same structural group (node 3), while megaloolithid oospecies from MG1, MG3, *M. maghrebiensis* and Faveoloolithus constitute a second sauropod eggshell group (node 4). On the other hand, eggshells attributed to theropod dinosaurs and extant birds are included in the same structural group (node 5). Finally, *Spheroolithus* eggshells are not placed in any group.

Results obtained with 50% majority-rule consensus analysis differ from the strict consensus tree in creating five additional nodes (Fig. 26B). The first new node involves turtle species. *Melanochelys trijuga* and *Malacochersus tornieri* always appear as out-group taxa while *Rhinoclemmys areolata* is placed in the next branch, in the 89% of the obtained trees. These three taxa constitute the out-group of archosaurian eggs. As occurred in the strict consensus tree, the Archosauria group (node 1) is strongly supported, occurring in 100% of resultant trees. A second new node, which appears in 67% of obtained trees, differentiates between Crurotarsi (crocodiles, node 2) and Avemetatarsalia (dinosaurs + birds, node 2') groups. Three branches can be observed within the last group, where two of them are nearly identical in the strict consensus tree results (nodes 4 and 5). The node 2'', which occurs the 67% of the times, groups

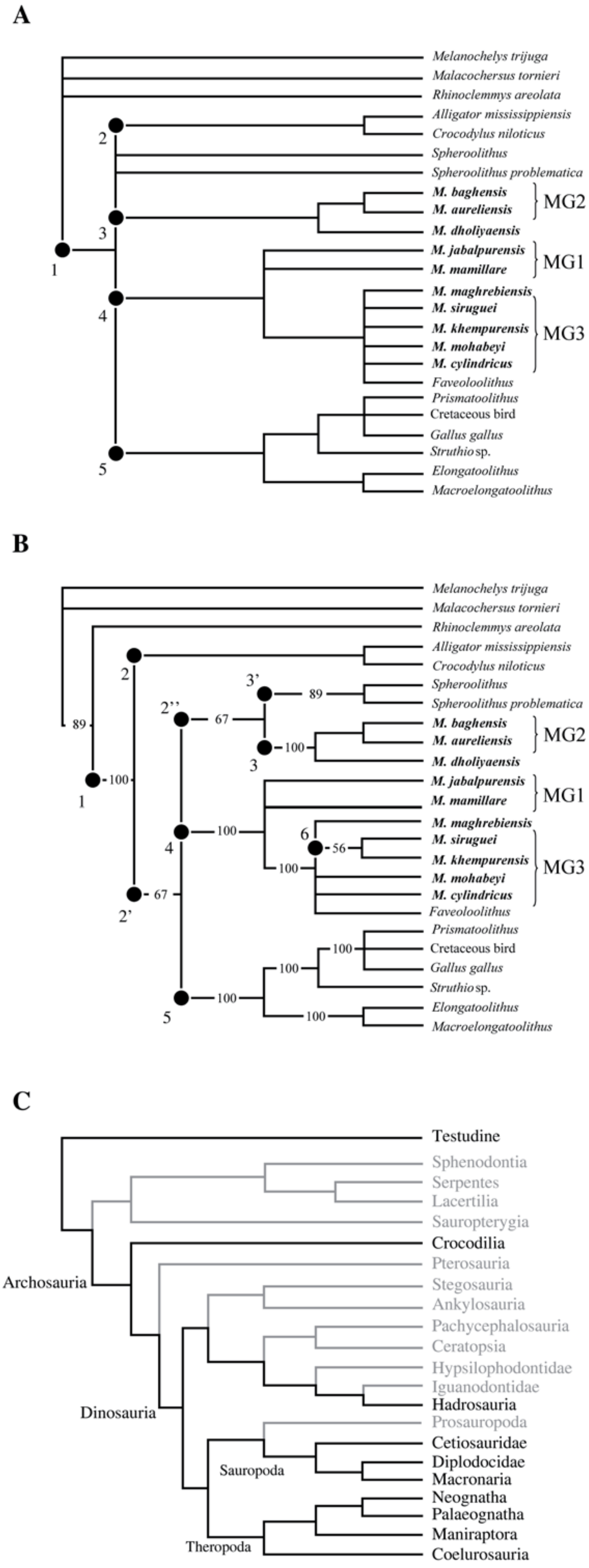

Figure 26. Pylogenetic results for megaloolithid eggs. A) Strict consensus tree, showing position of *Megaloolithus* oospecies and MG's groups. B) Majority-rule consensus tree of the shortest trees. C) Simplified phylogenetical tree of reptiles and birds. Nodes mark the position of each taxonomical/parataxonomical group: 1) Archosauria; 2) Crurotarsi (crocodiles); 2') Avemetatarsalia (dinosaurian + birds); 2'') Hadrosaur-like eggshells; 3) *Megaloolithus* from the MG2; 3') *Spheroolithus* (real hadrosaur eggs); 4) *Megaloolithus* from the MG1 and MG3 (real titanosaur eggs); 5) Theropoda; 6) "porous" megaloolithids.

MG2 group and *M. dholiyaensis* (node 3) and the *Spheroolithus* hadrosaur eggs (node 3'), which clustered in 87% of the resultants. Finally, the last node (node 6) involves the European *M. siruguei* and the Indian *M. khempurensis*, grouped the 56% of the times within the MG3 group.

6.1.2. Discussion of phylogenetic analysis

Although cladistic analysis based on oological remains (Fig. 26A, B) show some differences with phylogenetic trees based on taxonomical characters (Fig. 26C), they also exhibit some similitude with phylogenetic results based on skeletal remains, as was demonstrated previously (Grellet-Tinner, 2000, 2006; Varricchio and Jackson, 2004; Zelenitsky and Currie, 2004; Garcia *et al*., 2006; Grellet-Tinner and Makovicky, 2006; Winkler, 2006; Zelenitsky and Therrien, 2008; Jin *et al*., 2010).

MG1 group (*M. jabalpuriensis* + *M. mamillare*) is, now a day, the only group of megaloolithid eggs with an unequivocal relationship with sauropod dinosaurs (based on embryological remains). This group, together with MG3, *M. maghrebiensis*, and *Faveoloolithus* oogenus, could represent the group of sauropods. According to phylogenetic results, oospecies from MG3 would show more derived characters than those of MG1, even this does not imply a similar trend within its laying organisms.

M. maghrebiensis could be included in the MG3 group, because this oospecies always appears associated to that group of megaloolithid eggs, sharing many structural characters with the oospecies included in the MG3 group. Concerning *Faveoloolithus,* it appears as a sister group of MG3, attesting the previous idea of *Faveoloolithus* being related to sauropod dinosaurs. More interestingly, results suggest that faveoloolithid eggs could be a derived *Megaloolithus*.

The MG2 group appears as the sister group of the *Spheroolithius* oogenus, which belong to hadrosaurids. These results could have two explanations. In one hand, the assumption that the oospecies from the MG2 group belong to sauropods is a speculation, because since now no evidence for this relationship has been confirmed. Thus, this does not rule out the possibility that *M. baghensis* and/or *M. aureliensis* would be laid by another group of dinosaurs, such as hadrosaurs. In fact, Garcia (1998) hinted the possibility that the *M. baghensis* could be laid by *Rahbdodon*, a primitive ornithopod. Otherwise, if the relationship between oospecies of the MG2 group and sauropods is considered valid, it may indicate a significant amount of homoplasy in the evolution of structures that could strongly depend on the incubation environment, as well as the biology and the physiology of the reproductive system.

Finally, *Spheroolithus problematica* nov. com. appears as the sister ootaxon of *Spheroolithus albertensis* (*Maiasaura* egg), suggesting the presence of hadrosaur eggs in India. But this result is quite controversial, because no evidences of hadrosaurs have been reported from India so far.

6.2. Phylogenetical analysis of *Cairanoolithus*

As in the previous section, phylogenetic analysis of *Cairanoolithus* was conducted using the brunch-and-bound search algorithm of PAUP 4.0 software (Swofford, 1998) and considering 19 other ootaxa., which are coded according to Varricchio and Jackson (2004) and Jin *et al.* (2010). But here, three additional ootaxa have been codified according to literature description and by own observations: *Ovaloolithus* (Mikhailov, 1997; Bray, 1999; Zhang, 2010), *Faveoloolithus* (Mikhailov, 1997, Casadío *et al.*, 2002; Salgado *et al.*, 2007; Salgado *et al.*, 2009), and *Dendroolithus* (Mikhailov, 1997; Fang *et al.*, 2003, 2005). We decided to choose those oogenus because *Ovaloolithus* has been related to hadrosaurs (Mikhailov, 1997); *Faveoloolithis* is considered a sauropod egg oogenus (see results of section 5.1.2); *Dendroolithus* is a theropod egg (Kundrát *et al.*, 2007) with homoplasy with the dinosaur-spherulitic morphotype, such as *Megaloolithus* or *Spheroolithus*.

The data matrix includes 20 characters (See Appendix 3), 18 of which are referred to micro- and macrostructural characters of eggs and eggshells (character 1 to 17 and character 20). One of the other two characters is related with the ratio between egg size/adult size (character 18), while the other involves the arrangement of the egg within the clutch (character 19). As showed in section 5.1, some character stats have been modified from Varricchio and Jackson (2004) and Jin *et al.* (2010). Below, we discuss these characters and describe the character state for new ootaxa.

Varricchio and Jackson (2004) coded the composition of mammillary layer (character 4) in *Maiasaura* (*Spheroolithus*) and titanosaur (*Megaloolithus*) eggs as crystalline composition. Later on, Jin *et al.* (2010) coded them as unknown (character state 0). Here we agree with the first interpretation, given that all reptilian eggs show crystalline mammillary layer, excluding crocodiles, which exhibit organo-crystalline composition (Ferguson, 1985; Mikhailov, 1997). *Cairanoolithus, Ovaloolithus, Faveoloolithus* and *Dendroolithus* share the same character state as *Maiasaura* and titanosaur eggs.

Varricchio and Jackson (2004) and Jin *et al*. (2010) coded the form of crystals radiating from the base of the shell units (character 5) as: truncated, irregular or blocky. In contrast, in specialized literature, this character is mainly described as acicular, wedge-like and bladed-shaped or tabular (Hirsch, 1996; Mikhailov, 1997; Bray and Hirsch, 1998; Garcia *et al*., 2006; Grellet-Tinner and Mokavicky, 2006; Zelenitsky and Therrien, 2008; among others). For this reason we prefer to code character 5 according to the most common decryption in literature.

Similar dissertation is applied on character 16, which codes the type of ornamentation in the outer surface of eggshells. In Varricchio and Jackson (2004) and Jin *et al*. (2010) this character is coded as present (character state 0) or absence (character state 1). But we prefer to code this character specifying the type of ornamental pattern, such as smooth (character state 0), with ridges (character state 1), combining ridges and nodes (character state 2) or nodular (character state 3).

Finally, as proposed in the previous phylogenetic analysis, we added one new structural character (character 20) related to the fusion between adjacent shell units. Eggshells can show three states of fusion in shell unit: without fusion (character state 0), which is the primitive state in amniotes' eggshell (Deeming and Unwin, 2004); partial fusion between neighboring shell units (character state 1), which frequently take place in the upper half part of the shell units; complete interlock of shell units (character state 2), which difficult to dishing individual units.

Extant eggs of reptiles, such as turtles, lizards, snakes or crocodiles exhibit no-fused shell units. *Megaloolithus* and *Faveoloolithus* share the same condition (Mikhailov, 1997; Carpenter, 1999). Other types of dinosaur eggs show a partial fusion of shell units, such in *Dendroolithus, Spheroolithus, Ovaloolithus* and *Cairanoolithus* (Mikhailov, 1997, Carpenter 1999). Eggs of extant and extinct birds and fossil theropod (*Preprismatoolithus* and *Prismatoolithus, Elongatoolithus, Macroelongatoolithus* or *Laevisoolithus*) exhibit eggshells with a complete fusion of the shell units.

6.2.1. Results of the phylogenetic analysis

The phylogenetic analysis produced 48 maximum parsimony tree (tree length= 50, CI= 0.7, HI= 0.3, excluding one uninformative character (character 10); and RI=0.8256). The strict consensus tree (Fig. 27A) shows a well defined Archosauria group (node 1) and Chelonia group. This last represents the out-group. Two major groups are distinguished within Archosauria: the Crocodilia and the Dinosauria (node 2) groups. In one hand, the Crocodilia group, representing crocodiloid egg-type, shows that egg of *A. mississipiensis* can be considered sister taxa of *C. niloticus*. On the other hand, the Dinosauria group includes a well-defined branch defining the Theropoda group, which makes a politomy with *Faveoloolithus*, *Megaloolithus* and hadrosaurian eggs (*Spheroolithus* + *Ovaloolithus* + *Cairanoolithus*). In the Theropoda group (node 5), *Dictyoolithus hongpoensis* appears as the most basal theropod egg-type. *Dendroolithus,* previously assigned to oviraptorian therizinosaur, is placed out of the *Elongathoolithus* subgroup. *Oviraptor, Deinonychus* and large theropods eggs are included within this last group. *Preprismatoolithus,* TMF egg and *Prismatoolithus*, which are assigned to dromaeosaurian dinosaurs, represent evolving steps that gave place to *Ornithoid* egg-type group (node 6). This last group is represented by a triple politomy that includes eggs of Cretaceous birds, *Struthio* sp. and *Gallus gallus*.

The results obtained with 50% majority-rule consensus analysis (Fig. 27B) differ from the strict consensus tree in creating two additional nodes. The first new node, including hadrosaurian (*Spheroolithus* + *Ovaloolithus* + *Cairanoolithus*) and sauropod (*Megaloolithus* + *Faveoloolithus*) eggs, appears as a sister group of Theropoda group (node 5), which occurs in 75% of the obtained trees. The second additional node, present in the 63% of the obtained trees, comprises sauropod egg-types (node 3) and falls as a sister group of hadrosaurian eggs (node 4).

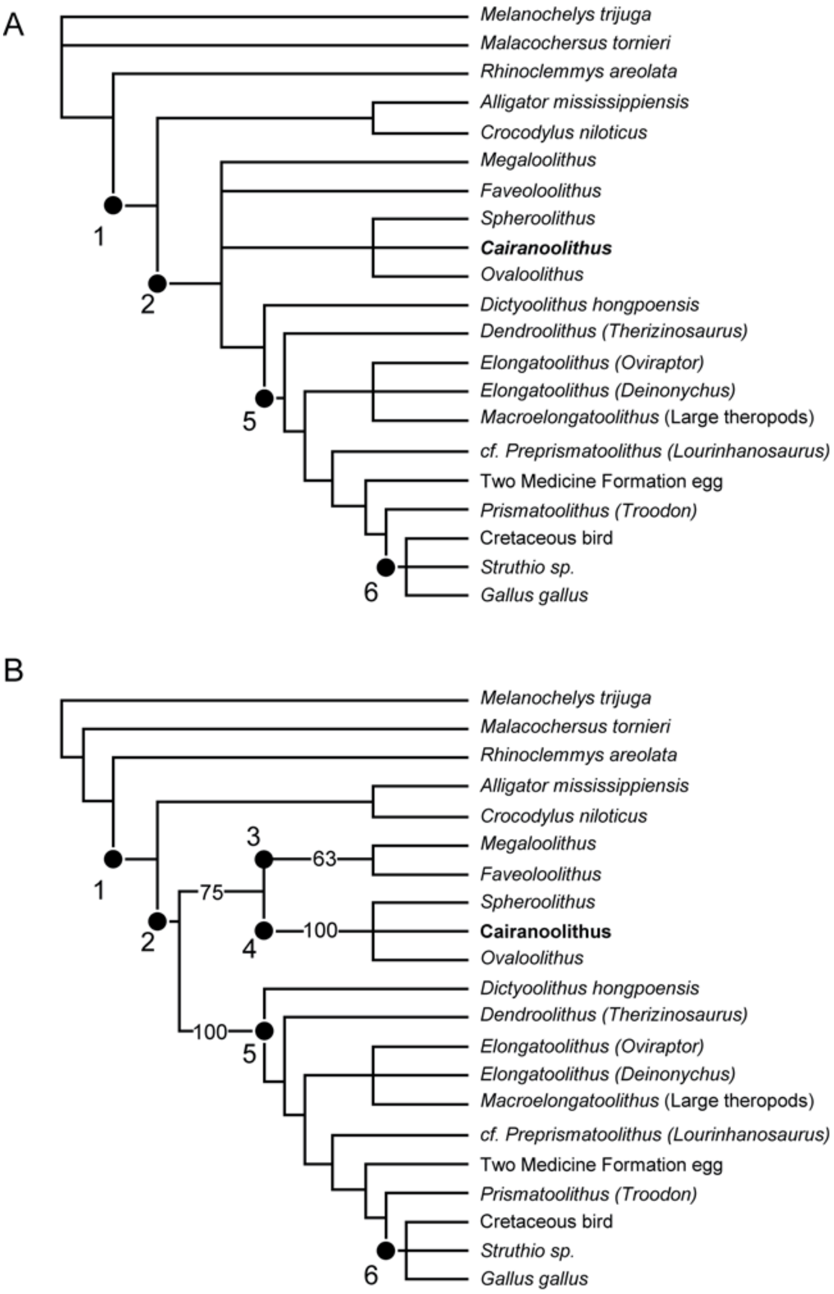

Figure 27. Phylogenetic results for megaloolithid eggs. A) Strict consensus tree, showing position of *Cairanoolithus*. B) Majority-rule consensus tree of the shortest trees. Nodes mark the position of each taxonomical/parataxonomical group: 1) Archosauria; 2) Dinosauria; 3) Sauropod ootaxa; 4) Hadrosaur ootaxa; 5) Theropoda; 6) Birds.

6.2.2 Discussion of phylogenetic analysis

Following the results obtained in the phylogenetic analysis, *Cairanoolithus* always appears placed as the sister ootaxon of *Spheroolithus* and *Ovaloolithus* oogenus. If this relationship is correct, and according to the taxonomical relationship between *Spheroolithus, Ovaloolithus* and ornithopod dinosaurs (Horner and Curry, 1994; Mikhailov, 1997; Horner, 1999, among others), it should mean that *Cairanoolithus* oogenus had to be also laid by ornithopod dinosaurs, such as hadrosaurs. However, our results differ from those of Garcia *et al*. (2006), where *Cairanoolithus* oogenus appeared in an intermediate position between *Spheroolithus* and *Megaloolithus*, placing *Cairanoolithus* at the base of Megaloolithae oofamily.

Anyway, the close relationship between eggshell microstructure exhibited by eggs of hadrosaurs and those of sauropod, would suggest a common origin or a significant amount of evolutionary convergence in some dinosaurian eggshell.

The monophyletic origin of dinosaurs is widely accepted (Benton, 2004), providing a common ancestor for all dinosaurs and at the same time, for their eggs microstructure. Contradictorily, according to current dinosaur phylogeny, hadrosaurs and sauropods belong to different groups, the first to Ornithischia and the others to Saurischia. From a taxonomical point of view, ornithischian and saurischian dinosaurs are too distant, but the differentiation between both groups toke place early in the evolutionary history of dinosaurs (Sereno, 1999). Eggshells from both hadrosaurs and sauropods exhibit primitive characters, such as mono-structural eggshells layer of fan-like shell units, also present in turtle and crocodiles. Thus, it would suggest that, at least, eggs attributed to hadrosaurs and sauropods could retain primitive condition of archosaurian eggs. On the other hand, the similitudes of the microstructure of eggs could also indicate a significant amount of homoplasy, which could strongly depend on incubation environment, feeding, as well as on the biology of the females and the physiology of their reproductive system.

6.2.3. Considering the taxonomical affinity of *Cairanoolithus*

Despite without embryonic remains associated to fossil eggs, previous result of Chapter 4.2.1 and 5.2 could though light on the taxonomical affinity of cairanoolithid eggs.

One of the first taxonomical approaches for *Cairanoolithus* was proposed by Garcia (1998). Assuming that both *Megaloolithus* and *Cairanoolithus* belonged to the same oofamily, she suggested that *Cairanoolithus* could be also produced by titanosaur sauropods. On the other hand, Cousin (2002) suggested that this ootaxon could be produced by *Rhabdodon*, a common iguanodontoid ornithopod during the Campanian and Early Maastrichtian in Western Europe.

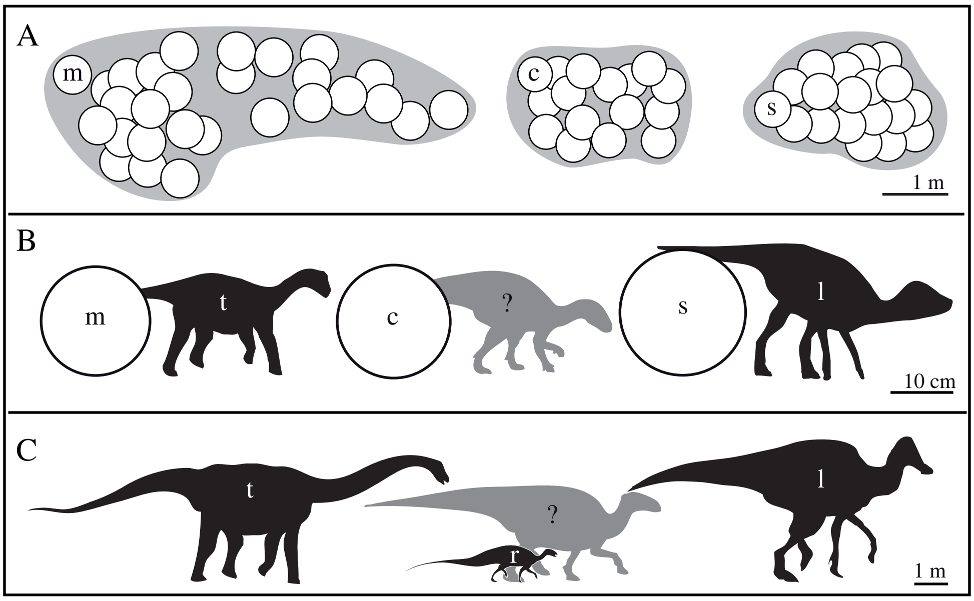

Figure 28. Comparison between clutches arrangement (A) (draws modified from Vila et al., 2010c; Cousin, 2002), egg and hatchling size (B), and probable egg-layier dinosaur adult size (C). c-*Cairanoolithus*; l- lambeosaur; m- *Megaloolithus*; r- *Rahbdodon*; s- *Spheroolithus*; t- titanosaur; ?- unknown ornithopod.

As previously was demonstrated, *Cairanoolithus* differs from *Megaloolithus*, being closely relates with *Sheroolithus* and *Ovaloolithus,* and suggesting an hadrosaurian affinity (see Horner and Currie, 1994; Mikhailov *et al*. 1994; Mikhailove, 1997, Horner, 1999; but see also Carpenter, 1999).

The big size of cairanoolithid eggs (15-18 cm in diameter) could constitute a problem, because it implies that this ootaxon would be related to big dinosaur, such as titanosaur. Horner and Currie (1994) reported big-sized eggs of *Spheroolithus* (approx. 20 cm in diameter), containing embryonic remains of *Hypacrosaurus* lambeosaur. Thus, the big size of lambeosaur eggs is unequivocal evidence that not only titanosaur could lay big sub-spherical eggs. It has been estimated that an egg of 20 cm of diameter produces a hatchling of 1 m long, which could grow up to 10 meters long when it was adult (Horner and Currie, 1994). If the same ratio is applied to *Cairanoolithus*, this could suggest that this ootaxon were laid by a dinosaur of about 8 meters long.

Unfortunately, all current known ornithopods from the Late Campanian- Early Maastrichtian of Spain and Franc are small-to-mid size. For example, *Rhabdodon* (Buffetaut and Le Loeuff, 1991) or *Tethyshadros* (Dalla Vecchia, 2009) were no longer than 5 meter (Fig. 28). For all these reasons the taxonomical affinity of *Caranoolithus* remains open.

SECTION 3

Oological diversity, temporal variability and taxonomical relationships

Chapter 7

OOLOGICAL DIVERSITY IN SOUTHERN PYRENEES

All the information recovered for the present study reveals an unexpected high diversity of fossil eggshell types in the Upper Cretaceous of Southern Pyrenees (Figs. 29, 30). These oological materials have been attributed to, at least, 13 different oospecies, which have been classified between six different oogenus, including *Megaloolithus* (Chap. 4.3), *Cairanoolithus* (Chap. 5.1), *Spheroolithus*, *Prismatoolithus, Pseudogeckoolithus* and *Ageroolithus* (Chap. 5.2).

The Megaloolithus oogenus, which is the best known group in the Pyrenees area, is represented by four valid oospecies (*M. aureliensis, M. siruguei, M. mamillare* and *M. baghensis*), present in the Àger and Tremp basins (Vianey-Liaud and López-Martínez, 1997; López-Martínez, 2000; Chap. 4.3) and the Coll de Nargó (Escuer *et al.*, 2006, Chap. 4.3) and the Vallcebre Synclines (Bravo *et al.*, 2005, Vila *et al.*, 2011). One cairanoolithid oospecies (*Cairanoolithus aff. roussetensis*) has been recognized in the Coll de Nargó Syncline (Chap. 5.1). This is the first report of the oogenus *Cairanoolithus* out of France, which was considered an endemic ootaxon from that region (Vianey-Liaud *et al.*, 2003). In the same way, the first *Spheroolithus* eggshells from the Upper Cretaceous of Europe are reported here. This material, probably representing a new oospecies, was found in Porri-6 site, in the Tremp Basin (Chap. 5.2).

On the other hand*,* *Prismatoolithus* oogenus is represented by six different oospecies. Vianey-Liaud and López-Martínez (1997) reported *P. matellensis, P. tenusi*, a new oospecies affine to *P. matellensis* and a probable new oogenus of prismatoolithid egg from Fontllonga-6 site (Àger Syncline). New oological material described in this thesis confirms the presence of a new ootaxon of *Prismatoolithus* in South Pyrenees, being present in Fonllonga-6 and in other many sites (see Chap. 5.2). Additionally, two new oospecies of *Prismatoolithus* have been recognized in La Massana outcrop (*Prismatoolithus* cf. *levis* and *Prismaoolithus*

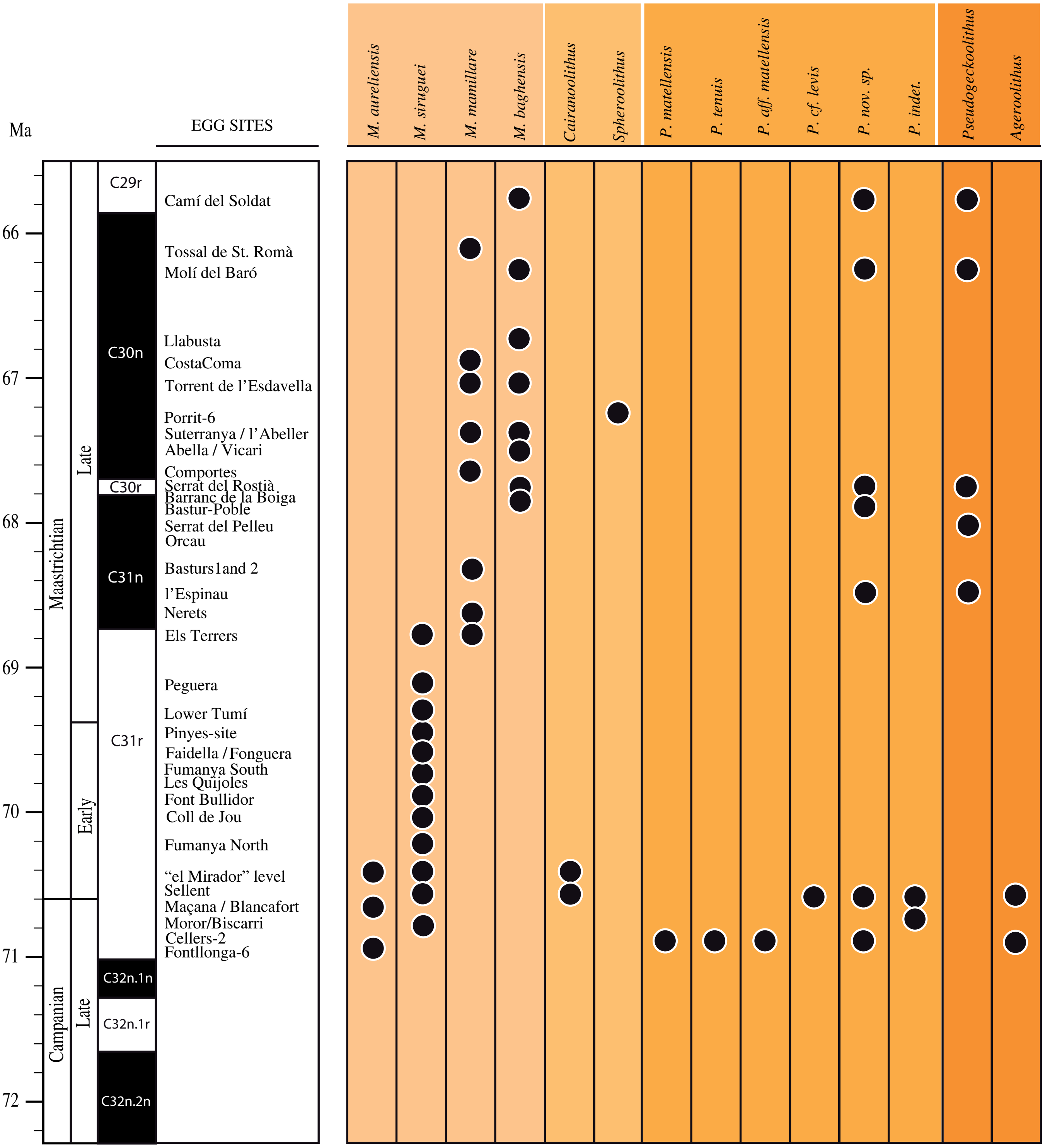

Figure 29. Stratigraphical distribution of egg sites in South-Central Pyrenees showing the oological contain per each site. Base on the absences of confect age of many site, they have been placed according to bioestratigrafical criteria

oosp. indet).

Only two eggshells, both from La Massana outcrop, have been described as ornithoid-ratite morphotype. The ratite oogenus *Ageroolithus* was described in Fonllonga-6 site (Vianey-Liaud and López Martínez, 1997), but it is also reported from the Upper Cretaceous deposits of France (Garcia, 2000) and from the Early Cretaceous of Galve (Teruel, Spain) (Amo-Sanjuan, 1998).

Finally, oological remains attributed to? *Pseudogeckoolithus*, which are represented by up to 800 eggshell fragments, have been found in some sites in the Àger and Tremp basins. This ootaxon was previously identified and described by Vianey-Liaud and López Martínez (1997) in Fontllonga-6 site (Àger Syncline) and tentatively referred to dinosauroid-prismatic morphotype. However, new oological material revealed a probable lizard origin for this ootaxon (see Chap. 5.2)

7.1. Comparison with other sites

Compared with other fossiliferous localities, the oological record of the South Pyrenees of Catalonia is similar to this of France (Tab.13). Vianey-Liaud and Crochet (1993), Vianey-Liaud *et al.* (1994), Garcia (2000) and Garcia *et al*. (2000) reported several different oospecies from many Upper Cretaceous sites of South France, including dinosauroid and bird types, and non-dinosauroid eggshells (e.g. turtles, geckonoid and crocodilian eggshells). The French oological list is composed of four prismatoolithid oospecies (*P. matellensis, P. tenuis, P. caboti* and *Prismatoolithus* oosp. indet.) and three ornithoid-type eggshells (*Ageroolithus, Levisoolithus*, and ?*Elongathoolithus*). According to the results obtained in Chapter 4.1.2, four valid oospecies of *Megaloolithus* (*M. aureliensis, M. siruguei, M. mamillare* and *M. baghensis*) could be identified in the Upper Cretaceous of France, while *Cairanoolithus* is represented by three ootaxa (Vianey-Liaud *et al.*, 1994; Garcia and Vianey-Liaud, 2001a, Cousin, 2002). Thus, the Upper Cretaceous of France contains at least, 13 different oospecies attributed to dinosaurs or relatives (e.g. birds). The oogenus *Pseudogeckoolithus* is also present in this region, but according to our result it cannot be considered as dinosaurian egg type.

Other Uppermost Cretaceous sites with abundant fossil egg material are less diverse than Southern France and Northern Spain ones (Table 13). For example, only five different types of dinosauroid eggshells have been reported from Peru (Vianey-Liaud *et al.*, 1997), and the same number of fossil egg-types has been found in Morocco (Vianey-Liaud and Garcia, 2003; Garcia *et al.*, 2003). The Two Medicine Formation of Montana (USA) has provided nine different types of dinosaur eggshells, while the Oldman Fm. of Alberta (Canada) has yielded eight different types of dinosaur's eggshells (see Jackson and Varricchio*,* 2010, and referenced therein). Late Campanian deposits of New Mexico (Tanaka *et al.*, 2011) and from Texas

	SPAIN	FRANCE	MOROCCO	PERU	NEW MEXICO	TEXAS	MONTANA	ALBERTA
Megaloolithus	4	4	2	1	-	-	-	-
Cairanoolithus	1	3	-	-	-	-	-	-
Spheroolithus	1	-	-	?	-	1	3	2
Prismatoolithus	6	4	1	-	2	1	2	2
Elongathoolithus	-	1	1	1	-	-	-	-
Ornithoid-type	1	2	1	2	2	4	4	4
TOTAL	13	13	5	5	4	6	9	8

Table 13. Comparison of the oodiversity reported from many site worldwide (see text for more details).

(Welsh and Sankey, 2007) are less diverse, with only four and six dinosaur egg-types have been respectively reported.

7.2. Temporal distribution in South Pyrenees: implications for taxonomical diversity, nesting site preference and environmental factors

Our results reveal that the oodiversity of South Pyrenees changed trough the time, being possible to distinguish three time intervals based on their relative oological diversity (Fig. 30A):

Interval-1: The oldest interval ranges from the Latest Campanian to the Earliest Maastrichtian. It involves the upper part of the Arén Sandstone Fm. and the major part of the Grey unit of the Tremp Fm. This interval shows the highest oological diversity recorded in Southern Pyrenees, represented by six to nine different types of fossil eggshells appertaining to five oogenus. The most common egg types during this time interval are *Prismatoolithus*, with six oospecies, and *Megaloolithus*, with two ootaxa. The unique oospecies of *Cairanoolithus* reported in Southern Pyrenees appears in the upper part of this first interval, co-existing with two oospecies of *Megaloolithus* in "El Mirador" Level, in the Coll de Nargó Syncline.

Interval-2: The oological diversity decreases dramatically in the middle interval. A single oospecies, *Megaloolithus siruguei*, is present from the Early Maastrichtian to the beginning of the Late Maastrichtian.

Interval-3: The youngest interval ranges from the upper part of the Lower Red unit of the Tremp Fm., which comprises four to five different ootaxa. *Megaloolithus* oogenus is represented by two oospecies (*M. mamillare and M. baghensis*) while *Prismatoolithus* is represented by one new ootaxon. The first *Spheroolithus* from Europe appears in a middle position within this last interval.

Similar temporal distribution of the oodiversity has been observed in Southern France. Garcia and Vianey-Liaud (2001b) noted that the oological diversity was maxima in the Upper Cretaceous, as occurs in south-central Pyrenees. They also observed the drastically decrease of the oodiversity during the Early Maastrichtian. This may suggest a possible relationship between oodiversity and the climatic changes that could occurr at this time. This climatic change can be interpreted from the study the palynological floras record (Ashraf and Erben, 1986).

Recently, Cojan and Moreau, (2006) have reported data about terrestrial climatic fluctuations in Provence. According to these authors the climate during the Campanian did not differ significantly from the subhumid climatic trend of the Upper Cretaceous. A semiarid episode has been documented near the Campanian-Maastrichtian boundary, followed by a cooling trend. After that, the climate fluctuated between warm and cold periods during the Maastrichtian (Cojan and Moreau, 2006). The drastic reduction of the oodiversity at the Early Maastrichtian could reflect that climatic change. The oofaunal recovery experienced during the Middle-Late Maastrichtian could be related with its relatively stable climate, which would propitiate a faunal adaptation.

Another possible way for explaining the differences in the oodiversity thought time could be related with environmental factors and preferences for the nesting site (Fig. 30B).

Most of prismatoolithid eggshells are preferably concentrated in the Grey unit, even they are also present in the upper half of the Lower Red unit. The Grey unit consist on coastal and lagoon deposits (Riera *et al*, 2009, and references therein), and *Prismatoolithus* recovered from the Lower Red unit mainly appear in oxbow lake (Molí del Baró site) or shallow lake environment (Camí del Soldat or l'Espinau sites; per. obs.). Apparently, dinosaur producers of prismatic-type eggs would have tend to lay their eggs in coastal zones or lacustrine areas. This appreciation is based on the recurrence of these ootaxa in lake and coastal deposits (see Zelenitsky and Hills, 1996; Varricchio *et al.*, 1997; Holtz, 1998; Garcia *et al.*, 2000; Zhao, 2003; Zelenitsky and Therrien, 2008, Liang *et al.*, 2009, among others). However, the laying of eggs would be taken place only during relatively dry seasons, which could interpreted from the pore system structure showed by these eggs (angusticanaliculate). Thus, they might be restricted to dry environments (Mikhailov, 1997; Carpenter, 1999; Deeming, 2006).

Concerning ornithopod eggs, both *Cairanoolithus* and *Spheroolithus*, appear in sandstones or limestone (e.g. Porri-6 and "El Mirador" level on Coll de Nargó area) associated to coastal environments. These observations are coherent with the widely accepted idea that hadrosaurs made their nest and laid their eggs in wet areas near the coastal line, as it has been interpreted in "Egg Mountain" site in Montana (see Horner and Makela, 1979; Horner, 1982, 1984; Horner and Currie 1994; Carpenter, 1999, Tanke and Brett-Surman, 2001, among others).

On the other hand, megaloolithid eggs dominate most of the Tremp Fm. excluding the Grey unit, where prismatoolithid eggshells are more common. According to our current knowledge on dinosaur nesting sites, megaloolithid eggs frequently appear linked to fluvial floodplains or near the crevasse-splay deposits adjacent to fluvial channels (Chiappe *et al.*, 2004; Cojan *et al.*, 2003; Therrien, 2005; Therrien *et al.*, 2009, among others). This relation is consistent with paleoenvironmental interpretations of sedimentological facies of the Lower Red unit of the Tremp Fm. (Riera, 2010).

A second possible interpretation for understanding the variations in the oological diversity of Southern Pyrenees could be the presence/absence of dinosaur fauna related with each type of fossil egg (Fig. 31).

- *Megaloolithus* oogenus shows a continuous record, from the Late Campanian to the end of the

Maastrichtian. Meanwhile, Sauropods are mainly present is South Pyrenees from the Early Maastrichtian to the Late Maastrichtian. However, the decreasing oodiversity during the Early Maastrichtian do not seem to be related with the absence/presence of sauropod fauna.

- *Spheroolithus* eggs have been attributed to hadrosaurs (Horner and Makela, 1979; Horner and Weishampel, 1988) and lambeosaurs (Horner and Currie, 1994) based on the embryonic remains found in North America and Canada. This group of dinosaurs was really abundant and diverse in the Upper Cretaceous of Pyrenees, being represented by both hadrosaurs and lambeosaurs (Pereda-Suberbiola *et al.*, 2009, Riera *et al.*, 2009). Spheroolithid eggshells from Porri-6 site were found associated to hadrosaur remains. However, the scarcity of hadrosaurian oological remains cannot be explained on the basis of the presence or absence of hadrosaurs in the fossil record.

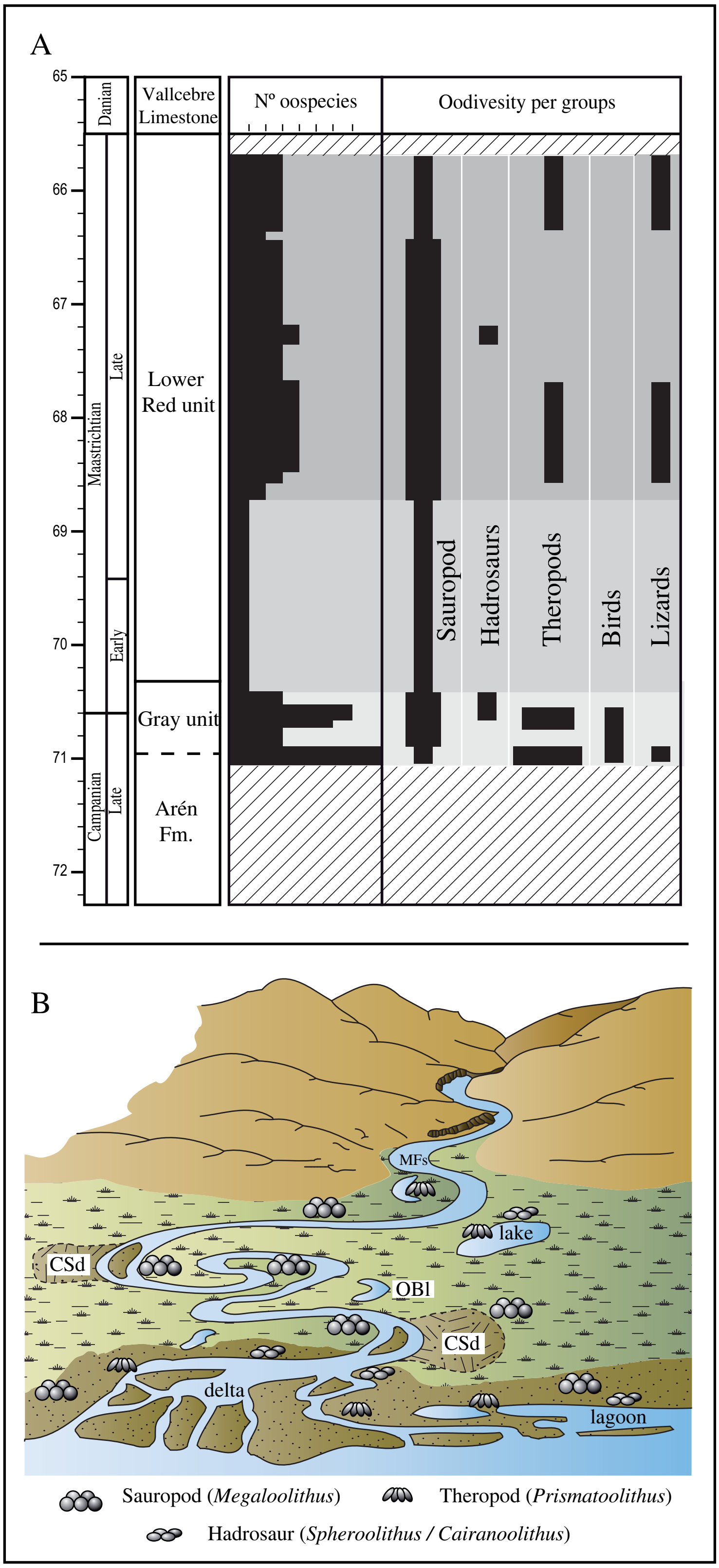

Figure 30. Oological diversity temporal (A) and spatial interpretation (B) distribution. Shaded area shows the absence of dinosaur fossil record.

- *Prismatoolithus* oogenus, which is related to some theropod dinosaurs such as *Troodon* (Horner and Weishampel, 1988, 1996; Carpenter, 1982) and *Oviraptor* (Norell *et al.*, 1994), is mainly concentrated in the Grey unit and also discreetly present in the Lower Red unit. Theropod remains are very scarce in the Upper Cretaceous of South Pyrenees, being represented by isolated teeth. Several teeth morphotypes have been described in the Tremp Fm. They have been classified in four major groups: *cf. Richardoestesia*, Coelurosauria, Dromaeosauria and Theropoda indet. (Pereda-Suberbiola, 1999; Prieto-Márquez *et al.*, 2000; Torices, 2002; Riera *et al.*, 2009). Most of these remains coincide in

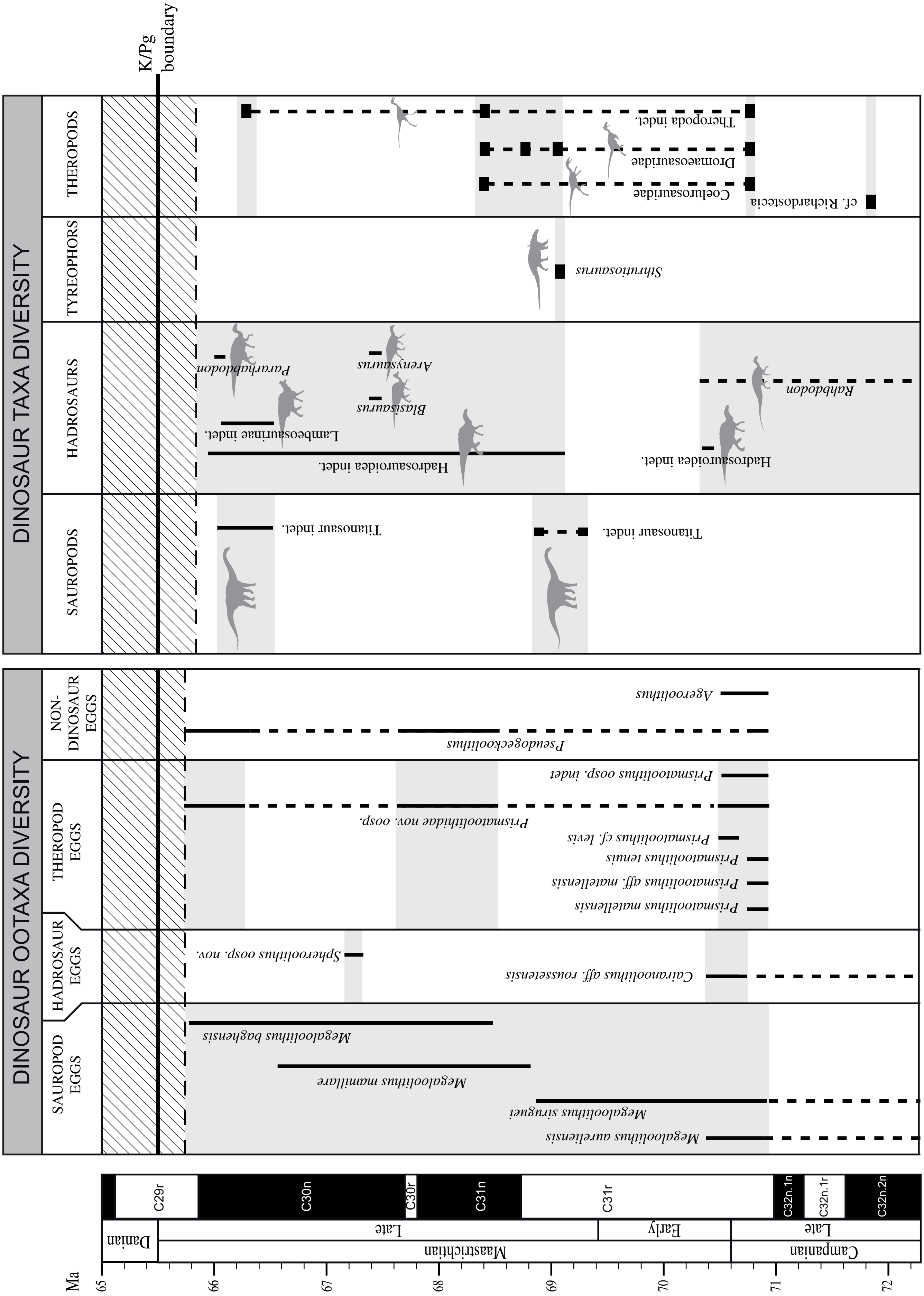

Figure 31. Schematic panel showing the correlatinon between oological and taxonomical record of dinosaurs in Southern Pyrenees. Grey areas infaticed the presenco of each record. Shaded area shows the absence of dinosaur fossil record.

time with low time difference with the oological material attributed to *Prismatoolithus* (e.g. Fontllonga-6 site). Unfortunately, the scarcity of theropod remains does not allow doing more dissertations about the variation of the oological record attributed to theropod dinosaurs.

Therefore, no consistent relationship could be established between the change in the oological diversity and the presence/absence of specific dinosaur fauna. On the other hand, it can be suggested that the current oological diversity of Southern Pyrenees could depend on sedimentary and environmental factors, reflecting preferences on the nesting area of each dinosaur group (Fig. 30B) or conditioned by climatic factors.

7.3. Possible taxonomical relationship between megaloolithid eggs and sauropod fauna in the Upper Cretaceous of Europe.

Panadès i Blas (2002) noted significant differences between the number of megaloolithid ootaxa and the sauropods of the Upper Cretaceous of Europe, being oospecies more numerous. In this section that question will be tried to solve, providing a possible relationships between each European *Megaloolithus* and the current known sauropod fauna from the end-Cretaceous time.

Without direct evidences (e.g. the presence of embryos within eggs or a close association between eggs and adults (see Horner and Makela, 1979; Bonaparte and Vince, 1979; Mateus *et al.*, 1997; Norell *et al.* 1994; Chiappe *et al.*, 1998; Horner, 1999; Reisz *et al.* 2005; Balanoff *et al.*, 2008; Sato *et al.*, 2005; Wilson *et al.*, 2010; Agnolin *et al.*, 2011, among others)) that allow to relate a particular type of fossil egg with its producer, it is difficult to assess the taxonomic attribution of these oological record.

Historically, *Megaloolithus* has been tentatively attributed to sauropod dinosaurs because both records appeared always associated (Erben *et al.*, 1979; Vianey-Liaud *et al*, 1987; Jain, 1989; Sahni *et al.*, 1994). However, Mikhailov (1997) suggested that a same fossil egg type could be produced by different dinosaurs (e.g. *Megaloolithus* could be laid by sauropods and hadrosaurs). Some authors agree with this argumentation (see Grigorescu, 2003; Grigorescu *et al.,* 2010), even it is widely accepted that each type of fossil egg must be related with a specific group of dinosaurs and may represent different major taxonomical groups within the same phylogenetic lineage (see Grellet-Tinner *et al.*, 2004, 2011; Garcia *et al.*, 2006). The discovery of ossified embryos inside megaloolithid eggs is an unequivocal evidence of the taxonomical relationship between *Megaloolithus* and macronarian sauropods (Chiappe *et al.*, 1998; Salgado *et al.*, 2005; Garcia *et al.*, 2006, 2010; Wilson *et al.*, 2010; Grellet-Tinner *et al.*, 2011). To date, none sauropod embryo has been found inside a megaloolithid egg in Europe.

Despite the difficulty of linking both oological and osteological records, here it is speculated a possible taxonomic affinity between European megaloolithid eggs and sauropods. For this approach, two factors must be considered: 1) the spatial distribution of taxa and ootaxa and 2) their temporal persistence. A couple taxon-ootaxon can only be considered linkable if both records have similar temporal and spatial distribution. Otherwise, the pair taxon-ootaxon should be rule out. Although an ootaxon and a taxon coincide in the temporal range, they could be rarely related if they are widely geographically separated (e.g. *Magyarosaurus* from Romania cannot be associated to *M. aureliensis* from Spain and France despite that taxa show a similar time range, because Romania was isolated from France and Spain during the Late Cretaceous). In Europe, fives species of sauropod from the Campanian to the Maastrichitan have been formally recognized: *Magyarosaurus dacus* (Nopcsa, 1915), *Ampelosaurus atacis* (Le Loeuff, 1995), *Lirainosaurus astibiae* (Sanz *et al.*, 1999), *Paludititan nalatzensis* (Csiki *et al.*, 2010), and *Atsinganosaurus velauciensis* (Garcia *et al.*, 2010). New additional material has been recently provided by Vila *et al.* (2012). On the other side, four valid oospecies of *Megaloolithus* are present during the same time interval in Europe: *M. aureliensis*, *M. siruguei*, *M. mamillare* and *M. baghensis* (Fig. 32).

During the Late Campanian, two oospecies of *Megaloolithus* coexisted for a long time: *M. aureliensis* and *M. siruguei*. *M. aureliensis* is present in Northern Spain and Southern France, while *M. siruguei* is also reported from Romania. For the same time period, two titanosaurs taxa have been recognized: the French *Atsinganosaurus velauciensis* (Garcia *et al.*, 2010) and *Lirainosaurus astibae* (Sanz *et al.*, 1999), present in Spain and France (Vila *et al.*, 2012). Apparently, both taxa could be related to any of the oospecies, given they mach temporally and geographically.

Atsinganosaurus veluciensis, a primitive titanosaur, was discovered less than 8 meters below an eggshell-site in Velaux-La Bastide Neuve (Garcia *et al.*, 2010, see Fig. 1). However, only one oospecies of *Megaloolithus*, *M. aureliensis* (Garcia, 1998) has recovered from that site. Due that both *Atsinganosaurus veluciensis* and *Megaloolithus aureliensis* occur in the same time and place, it could be reasonable to link both records.

On its turn, *Lirainosaurus astibae* is a common titanosaur from Spain. This dinosaur and *Megaloolithus siruguei* have been commonly recovered from the same geological units in both Spain (Alonso *et al.*, 1991; Moratalla, 1993; Company, 2008; Ortega *et al.*, 2008) and France (Garcia, 1998; Vila *et al.*, 2012). Even, cf. *Lirainosaurus* has been also recognized in Bellevue Farm site (Villa *et al.*, 2012), it never provided oological material. Anyway, the co-occurrence of these two records might suggest that *M. siruguei* could be tentatively related to *Lirainosaurus*.

Only one *Megaloolithus* oospecies (*M. siruguei*) is reported from the Early Maastrichtian and the beginning of the Late Maastrichtian in Europe. Sauropod fauna is represented by, at least, three formally recognized taxa:

Magyarosaurus dacus (Nopsca, 1915), *Paludititan nalatzensis* (Csiki *et al.*, 2010) and *Ampelosaurus atacis* (Le Loeuff, 1995). *Paluditian* and *Magyarosaurus* are endemic taxa from Romania, while *Ampelosaurus* was found in France. Romania has only provided oological material assigned to *M. siruigie*; therefore, there is only one possible linkage between Romanian sauropods and this oospecies. *Ampelosaurus atacis* was discovered in Bellevue Farm site (Le Loeuff, 1995), where non-oological material has been recovered. However, given that *M. siruguei* is the only ootaxon present during the Early Maastrichtian, it seems plausible to relate *Ampelosaurus atacis* and *Megaloolithus siruguei*. Thus, these two fossil records appear frequently associated, suggesting a possible relationship between *M. siruguei* and new titanosaurs from Southern Pyrenees.

Given that the eggshell is a very conservative and high stable structure within major taxonomical groups, one oospecies, such as *Megaloolothus siruguei,* could be associated to more than one species, all of them phylogenetically related. Given that most of European sauropods from the Early Maastrictian, such as *Lirainosaurus, Ampelosaurus* or *Magyarosaurus*, have been classified as basal lithostrotian (Sanz *et al.*, 1999; Wilson, 2002; Curry-Rogers, 2005; Csiki *et al.*, 2010; among others), here it is proposed to relate this group of sauropods to the oospecie *M. siruguei.*

Finally, two megaloolithid oospecies coexisted during the major part of the Late Maastrichtian: *M. mamillare* and *M. baghensis*. Currently, there is no formally described sauropod in Europe for this time period. However, this group of dinosaurs has been recently reported by some appendicular elements from Southern Pyrenees (Vila *et al.*, 2012). The preliminary results obtained by these authors suggest the presence of four different forms of advanced titanosaurs in the Late Cretaceous of Southern Europe. Most of the sites yielding sauropod remains also provided eggshell fragments attributed to *M. mamillare* or *M. baghensis* (e.g. Peguera-1, Molí del Baró and Presa de Tremp see Moratalla, 1993, Vila *et al.*, 2011, Chapter 4.3).

To date, only oospecies of MG1 group (see Chapter 4.1.2) could be indubitably associated with titanosaurs (Chiappe *et al.*, 1998, 2001, 2005a, b; Wilson *et al.*, 2010). Chiappe *et al.* (2005a, b) and García *et al.* (2010) suggested that embryos remains associated to *M. jabalpurensis* (=*M. patagonicus sensu* Calvo *et al.*, 1997) shared many characters with advanced titanosaurs, such as *Alamosaurus*, *Nemegtosaurus* or *Saltasaurus*. Given that *M. jabalpurensis* is considered the sister ootaxa of *M. mamillare* (see Chapters 4.2 and 6.1.), it could be suggested that *M. mamillare* would be also laid by advanced titanosaurs.

Despite the relatively high amount of oological material referred to *M. baghensis* and the scarcity of sauropod remains for the same time in Europe, it is difficult to hypothesize about the possible relationship of these oospecies and any particular group of sauropods. However, a tentative approach could be done based on the co-occurrence of this oospecies and titanosaurs in South America. *M. baghensis* has been reported from

Brazil (Grellet-Tinner and Zaher, 2007), Peru (Vianey-Liaud *et al.*, 1996) and Argentina (Salgado *et al.*, 2007). No sauropod remains have been recovered from the same geological formation in Peru, even they are abundant in Brazil and Argentina (Novas, 2009). Most of the Upper Maastrichtian titanosaurs from the Marília Fm. of Brazil (e.g. *Aeolosaurus, Barurutiutan, Uberabatitan* and *Trigonosaurus*) have been included in the phylogenetical group Aeolosaurinae (see Salgado and Carvalho, 2008 and reference herein), but saltasaurines are not present. On its turn, the Maastrichtian Allen Fm. of Argentina has yielded diverse titanosaur taxa (e.g. *Aeolosaurus, Rocasaurus, Bonatitan* and *Antarctosaurus*) (see Garcia and Salgado, 2012 and reference herein). Thus, two major groups of titanosaurs can be distinguished within this formation, aeolosaurines and saltasaurines. Considering that saltasaurines, as advanced dinosaurs, have been linked to *M. mamillare*, aeolosaurines could be related with *M. baghensis*. However, no evidences of aeolosaurin titanosaurs have been reported from the Late Maastrichtian of Europe. Thus, the taxonomical affinity of *Megaloolithus baghensis* stays unresolved.

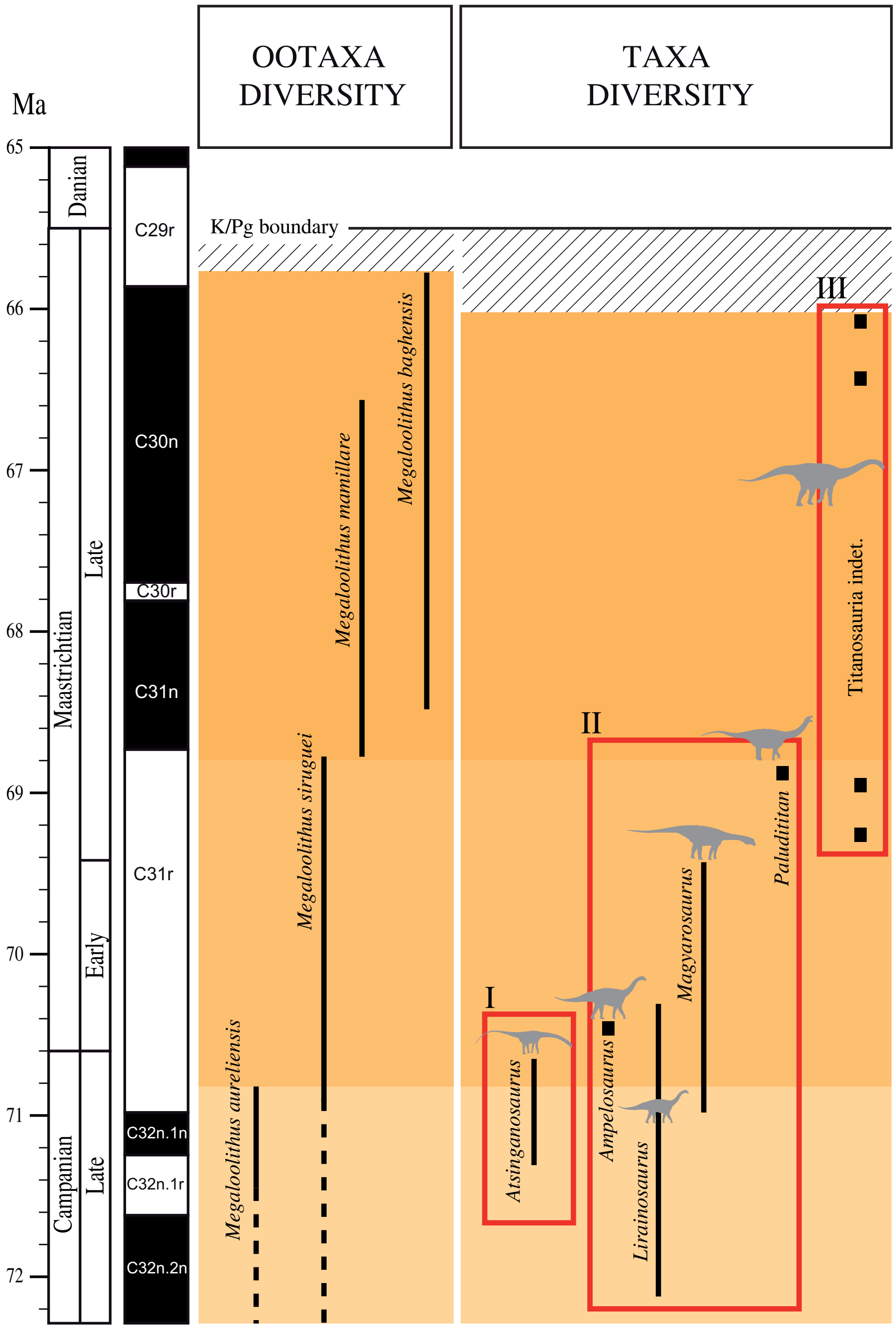

Figure 32. Schematic panel showing the possible correlation between each oospecies of Megaloolithis and particular group of sauropod fauna in South Europe. I-Basal titanosaurs, II-Basal lithostrotian, and III-Advanced titanosaurs. Shaded area marks the absence of both dinosaur and egg fossil records.

Thus, it can be concluded that *Megaloolithus aureliensis* could be related with basal titanosaurs, such as *Atsinganosaurus;* meanwhile the oospecies *Megaloolithus siruguei* could be linked to basal lithostrotian sauropods (e.g. *Ampelosaurus, Lirainosaurus* or *Magyarosaurus*), and *Megaloolithus mamillare* to advanced titanosaurs (see Fig. 32). Finally, the possible relation between *Megaloolithus baghensis* and aeolosaurin titanosaurs could be suggested in South America, but it cannot be confirmed in Europe.

Once again, it will be important to note the speculative character of results obtained in this section, even they could represent a starting point for a future new line of research.

SECTION 4

Biostratigraphical implications

Chapter 8

BIOESTATIGRAPHY OF THE UPPER CRETACEOUS OF SOUTHERN EUROPE BASED ON THE *MEGALOOLITHUS* OOSPECIES SUCCESSION

The Upper Cretaceous continental deposits of South and South-Eastern France have yielded different types of dinosaur eggshells (Dughi and Sirugue, 1957; Kerourio, 1981, 1982; Williams *et al.* 1984; Vianey-Liaud *et al.*, 1994; Garcia, 1998, 2000; Garcia and Vianey-Liaud, 2001b; Garcia *et al.*, 2003a; Bousquet and Vianey-Liaud, 2001;). On the base of the occurrence of several oospecies distributed into stratigraphical sections in five different areas at South France, French palaeontologists suggested the utility of eggshells as biochronological markers (Garcia, 2000; Garcia and Vianey-Liaud, 2001a, b; Garcia *et al.*, 2003a, but see also Peitz, 2000a). Vianey-Liaud and López-Martínez (1997) studied the temporal succession of Late Cretaceous dinosaur eggshells from the Tremp Basin (Southern Pyrenees) and compared it with the proposed biostratigraphic succession of Provence and Languedoc (South France), recognizing three successive eggshell assemblages in both areas. Recently, a similar biochronological study has been carried out in the Vallcebre Syncline (Bravo *et al.*, 2005; Vila *et al.*, 2011), redefining some limits between egg assemblages.These works show that the Campanian and the Maastrichtian continental deposits in South Pyrenees and Provence are the most continuous in Europe and can be unambiguously correlated with standard geomagnetic polarity time scale.

8.1. INTRODUCTION

The importance of the fossil eggshell record falls in the fact that they can be used as biochronological tool in sediments poor in other chornostratigraphical markers, such as pollen, charophytes or ostrachods. In this chapter is established the biostratigraphy based in the megaloolithis oospecies succession in the Coll de Nargó Synceline and the Àger and Tremp basins and inferred the age of these areas. Moreover, it will be proposed a general and standard European megaloolithid biostratigraphy for the Upper Cretaceous continental deposits.

8.2. BIOSTRATIGRAPHY AT PINYES NESTING AREA (COLL DE NARGÓ SYNCLINE)

At Pinyes nesting site dinosaur eggs and clutches appear distributed along 30 consecutive stratigraphic levels of a stratigraphical section of 370 meters. Reiterative occurrence of megaloolithid eggs and eggshells at Pinyes site has allowed establish an egg succession along more than 320 meters of continuous continental deposits (see Fig. 33A).

The lateral sampling of one level situated at 22 m of the base of the stratigraphic section, known as "El Mirador" level, has revealed the co-occurrence of three oospecies (*Cairanoolithus aff. roussetensis*, *M. siruguei* and *M. aureliensis*). This association resembles the Assemblage 1 defined by Garcia and Vianey-Liaud (2001b) in South France, which is characteristic from the Late Campanian – ?Early Maastrichtian. This assemblage was partially identified in the Tremp Basin (Vianey-Liaud and López-Martínez, 1997), being only composed by *M. aureliensis*, even it has not been reported in the neighbour basin of Vallcebre Syncline (Vila *et al*., 2011).

Only one oospecies (*M. siruguei*) is recognized along the major part of the stratigraphic succession (up to 170 m). The Assemblage 2 of Garcia and Vianey-Liaud (2001b), which was characterized by "including only *M. siruguei*, possibly the last *M. petralta*, and the first *M. mamillare",* could be equivalent to Pinyes monospecific record of *M. siruguei*. Similar association has been reported in the Aix Basin and in Corbiere-Aude Vally area in South France (Garcia and Vianey-Liaud, 2001b). Base in the oological and magnetostratigraphic records from the Vallcebre Syncline (South-Central Pyrenees), Vila *et al*. (2011) suggested that the Assemblage 2 finishes with the first occurrence of *M. mamillare*.

The last oological remain in Pinyes site is represented by an isolate specimen of *M. baghensis*, which could resemble the Assemblage 3 of Garcia and Vianey-Liaud (2001b). According to French authors, this assemblage was characterised by the only possible co-occurrence of *M. mamillare* and *M. baghensis* (=*M. pseudomamillare* after Vianet-Liaud *et al*., 2003). But *M. mamillare* is not reported in Pinyes nesting area. Nevertheless, the absence of this oospecies between *M. siruguei* and *M.baghensis* has been also observed in Maupague and Vitrolles Le Porry sections of Aix Basin and in Corbiere-Aude Vally area in Southern France (Garcia and Vianey-Liaud, 2001b), suggesting that *M. mamillare* could not be present in the third assemblage and leaving *M. baghensis* as the only representative of Assemblage 3.

Comparing the biostrigraphical results from the Coll de Nargó Syncline from those of south-eastern France, a significant difference can be observed. In Pinyes nesting area (Coll de Nargó Syncline) the last occurrence of *Cairanoolithus* oogenus coincides with the last presence of *M. aureliensis* (Fig. 33A), while in France this event could occurs with the last record of *M. petralta* (Garcia and Vianey-Liaud, 2001b, see Fig. 33B). However, considering that *M. petralta* could be a junior synonymous of *M. aureliensis* (see Chapter 4.1.2), then *M. aureliensis* and *Cairanoolithus* oogenus could disappear from the fossil record at the same time, both in Northern Spain and in Southern France. This event marks the upper limit of the lower megaloolithid assemblage (Fig. 33B), which is established near the transition between chrones C32 and C31 (Garcia and Vianey-Liaud, 2001b), in the Late Campanian (Husson *et al.*, 2011).

On the other hand, the presence of *M. baghensis* suggests that the upper part of the oological succession in the Coll de Nargó Syncline could be dated as Late Maastrichtian (chrone C31n).

Therefore, despite the absence of more chronostratigraphical data, our biostratigraphical results on *Megaloolithus* succession suggest that Pinyes nesting area ranges from the Later Campanian (C32n.1n) to the Late Maastrichtian (C31n) (Fig. 33C).

These results confirm the usefully of megaloolithid oospecies as biostratigraphical markers for the Upper Cretaceous continental deposits. However, here we want note an inappropriate use of terminology applied to megaloolithid biostratigraphy. Garcia and Vianey-Liaud (2001b) used the term “Assemblage” to refer each ootaxa association, which included two or more oospecies. But this definition cannot be applied in the “Assemblage 2” (after Vila *et al.*, 2011), which is exclusively composed by *M. siruguei*, because results obtained in Coll de Nargó Syncline and in Vallcebre Syncline. For this reason we prefer to use the term “Oozone” understood as interval of time defined on the basis of a single ootaxon or combinations of ootaxa, or variations in features related to the distribution of fossil eggshells.

Therefore, from now we will talk of:

1) ***Megaloolithus aureliensis* oozone**: referred to first association composed by the possible co-occurrence of *M. aureliensis, C. roussetensis* and *M. siruguei*, which could be considered equivalent to Assemblage 1 *sensu* Garcia and Vianey-Liaud (2001b).

2) ***Megaloolithus siruguei* oozone:** characterised by the monospecific occurrence of *M. siruguei*, corresponding to Assemblage 2 of Garcia and Vianey-Liaud (2001b) and according to Vila *et al.* (2011).

3) ***Megaloolithus mamillare* + *Megaloolithus baghensis* oozone:** represented by the possible co-occurrence of *M. mamillare* and *M. baghensis*, being equivalent to Assemblage 3 of Garcia and Vianey-Liaud (2001b).

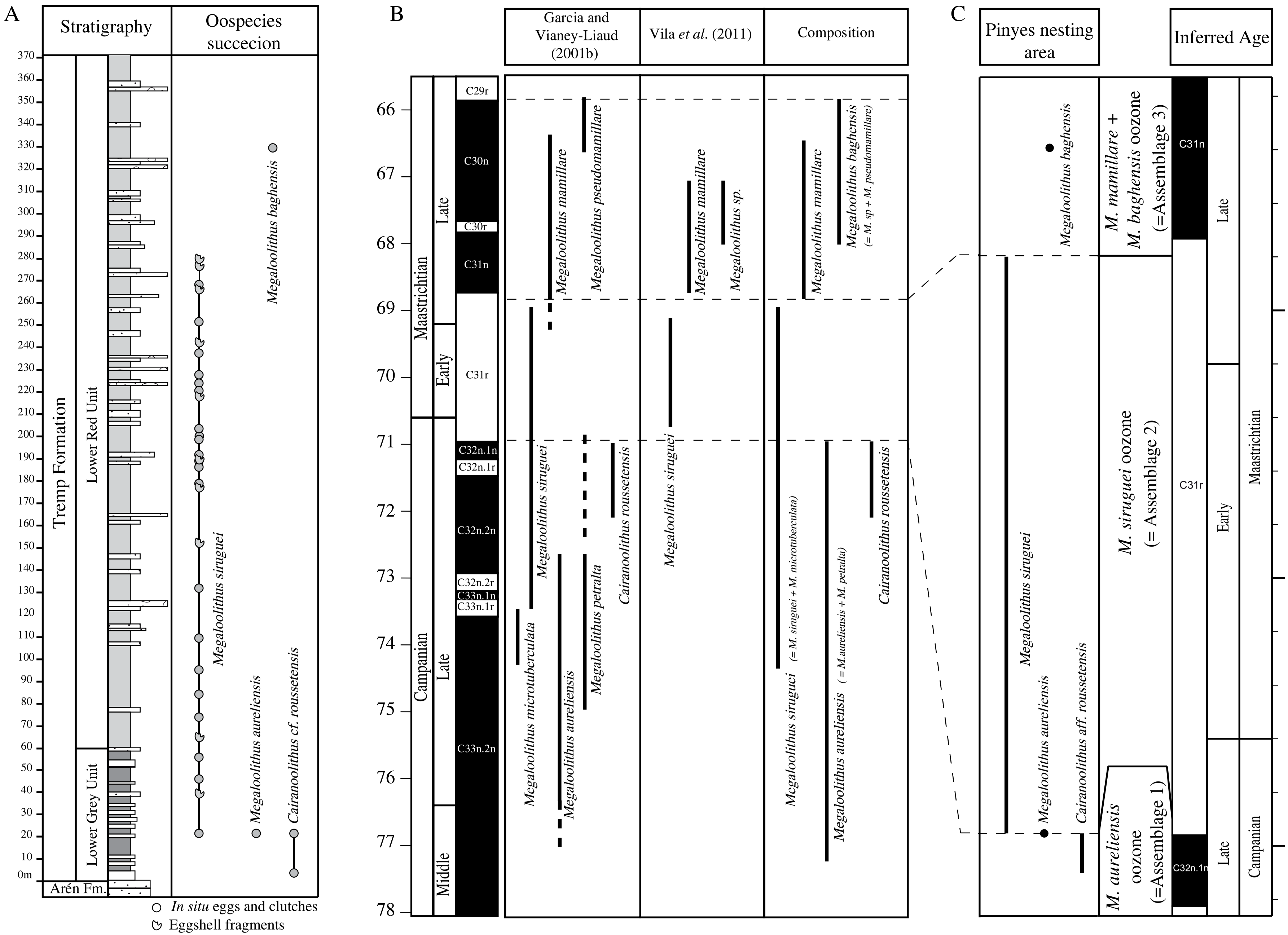

Figure 33. Biostratigraphical panel of Coll de Nargó Syncline. A) Stratigraphical section showing the occurrence of each oospecies. B) Comparison and combination of different biostratigraphical successions (see text for more details). C) Biostratigraphical successions of *Megaloolithus* in Coll de Nargó Syncline and its inferred age.

8.3. BIOSTRATIGRAPHY OF THE ÀGER AND TREMP BASINS

As occurs in other basins of Southern France and North Eastern Spain, each oospecies of *Megaloolithus* found in the Àger and Tremp basins is present for a specific range in the stratigraphical section of the Upper Cretaceous, being possible to distinguish three megaloolithid oozones (Fig. 34A)

In the Àger and Tremp basins, the lower egg assemblage is represented by the presence of *M. aureliensis* and *M. siruguei*. First oospecies has been reported from Blancafort site and it was previously recognized in Fontllonga-6 and Moror sites (Vianey-Liaud and López-Martínez, 1997; López-Martínez, 2000), while second oospecies occurs exclusively in Biscarri sites (Moratalla, 1993; López-Martínez, 2000). The age of Fontllonga-6 site is established near the limit between C32n.1n and C31r (Galbrun *et al*, 1993; Galbrun, 1997; Vianey-Liaud and López-Martínez, 1997; López-Martínez, 2000, 2003), which is placed in the Lattermost Campanian (Husson *et al.*, 2011). The presence of *M. aureliensis* oospecies suggests that the lower egg assemblage in the Àger and Tremp basins corresponds to *M. aureliensis* oozone, according to the new terminology proposed previously. But in the Àger and Tremp basins, the *M. aureliensis* oozone differs from those of the Coll de Nargó Syncline and equivalent Assemblage 1 from France (*sensu* Garcia and Vianey-Liaud, 2001) in the absence of *Cairanoolithus* oogenus.

The middle oozone in the Àge and Tremp basins is composed exclusively by *Megaloolithus siruguei*, which has been reported from Barranc de la Fonguera and Coll de la Faidella sites (Bravo *et al.*, 2000; López-Martínez, 2003). Even *M. siruguei* is not the most common ootaxon in Tremp area, this oospecies occurs along more than 100 m in the stratigraphical section, covering most of the lower part of the Tremp Fm. No confident data for the ages of these sites has been provided, but they have been tentatively dated as Early Maastrichtian (see Bravo *et al.*, 2000; López-Martínez, 2000, 2003). The *M. siruguei* oozone in Àger and Tremp basins is equivalent to those of the Coll de Nargó Syncline and the Vallcebre Syncline (Vila *et al.*, 2011) from Southern Pyrenees and Assembage 2 (after Vila *et al.*, 2011) proposed by García and Vianey-Liaud (2001) in Southern France (Fig. 33.B)

The uppermost assemblage in the Àger and Tremp basins is composed by *Megaloolithus mamillare* and *Megaloolithus baghensis*. These oospecies mainly appear stratigraphicaly separated, but they could be associated in the same site, as has been reported in Suterranya, l'Abeller and probably in Orcau site (see Moratalla, 1993). Precise dating of these sites is still unclear. However, based in charophytes succession established in neighbor sites where *M. mamillare* and *M. baghensis* appear, Feist and Colombo (1983) attributed them a Late Maastrichtian age. Additionally, according to stratigraphical and magnetostratigraphical data reported by Riera *et al.* (2009) in the Tremp Basin, the upper part of the lower Tremp Fm. could falls between

C31n and C30n chrones. The *Megaloolithus mamillare* + *Megaloolithus baghensis* oozone are consistent with Assemblage 3 defined in Aix-en-Provence Basin by Garcia and Vianey-Liaud (2001), and similar to those reported in Vallcebre Syncline (Vila *et al*., 2011); but it differs from those of Coll de Nargó Syncline, because in this last area the oospecies *M. mamillare* is not present.

8.4. CONSIDERATIONS ABOUT THE BIOSTRATIGRAPHY IN THE VALLCEBRE SYNCLINE

Vila *et al*. (2011) provided one of best controlled biostraigraphy based on megaloolithid oospecies succession in Europe, which is magnetostraigraphicaly calibrated. Two assemblages were identified in the Vallcebre Syncline and results of that study updated the information about oological chances between Assemblages 2 and 3.

The lower assemblage (Assemblage 2 *sensu* Vila *et al*., 2011) is composed exclusively by *M. siruguei*, suggesting that this assemblage can be included in the *M. siruguei* oozone. The upper assemblage in the Vallcebre Syncline was considered equivalent to Assemblage 3 from France (see Vila *et al*., 2011). However, this assemblage was formed by the presence of *M. mamillare* and an indeterminate *Megaloolithus* oospecies.

A review of the oological material referred to *Megaloolithus* sp. (J-BAR01 and E-MUN06, in Vila *et al*., 2011) from the Vallcebre Syncline shows that this indeterminate oospecies can be re-assigned to *M. baghensis*, because they exhibit similar structural characters, such as shell thickness, ornamental pattern composed of coalescent nodes and the shape of the partial-fused shell units.

According to this new interpretation, the Assemblage 3 (sensu Vila *et al*., 2011) would be finally composed by *M. mamillare* and *M. baghensis*, being attributable to *M. mamillare* + *M. baghensis* oozone (see Fig. 35A).

8.5. UPDATING THE EUROPEAN MEGALOOLITHID BIOCHRONOLOGY

According to new information and data of biostratigraphical base on *Megaloolithus* succession in the Upper Cretaceous of South Pyrenees; it is updated the current European megaloolithid biostratigraphy.

Despite the great number of sites yielding eggs and eggshells of *Megaloolithus* beyond the Pyrenees (e.g. Burgos, Valencia and Cuenca provinces), most of them are not considered is the following work because the lack of confident dating of these sites.

Most of Upper Cretaceous egg-sites is North Spain are located in the south-central Pyrenees, but one egg-site has been found in southwestern Pyrenees. López-Martínez *et al.* (1999, 2001) reported a single eggshell that, according to the author, could be similar to *M. pesudomamillare*, which is considered a junior synonymous of

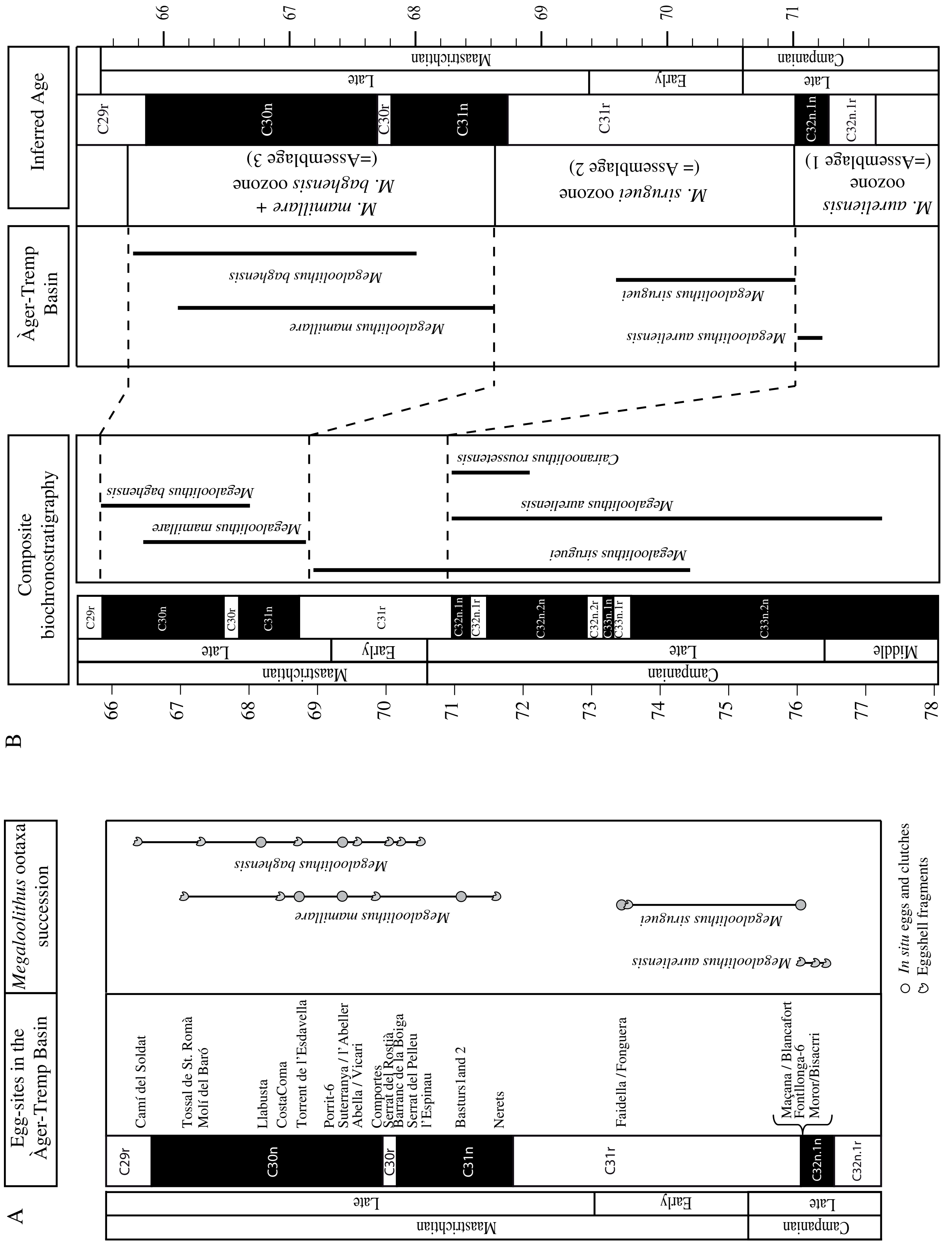

Figure 34. Biostratigraphical panel of tha Àger and Tremp basins. A) Chronological succession showing the situacion of each site and the occurrence of each oospecies. B) Combinated biostratigraphical (see Fig. 37 and text for more details). C) Biostratigraphical successions of *Megaloolithus* in Àger and Tremp basins and its inferred age.

M. baghensis (Vianey-Liaud *et al*., 2003), in Blasi-2 site (Huesca province, Aragon). A review of that material suggests a possible misinterpretation on the microstructural characters of the eggshell. According to own observations, eggshell from Blasi-2 belongs to crocodiloid morphotype, because it exhibits truncate-cone-like shell units with a bulbous base and irregular rough wedges (see López-Martínez, 2003, plate1). Additionally, pore apertures observed in that eggshell are similar of those exhibited by eggshells of alligators (Ferguson, 1985). Thus, oological material from Blasi-2 in not included in our biostratigraphical study.

Below, they are defined the three major megaloolithid oozones base on the egg-assemblages present in Northeaster Iberian Peninsula and Southwester Farce, and considering the Romanian sites (Fig. 35C).

1) *Megaloolithus aureliensis + Cairanoolithus oozone:* The lower assemblage is characterized by the possible co-occurrence of *M. aureliensis, M. siruguei* and *Cairanoolithus* oogenus. The most complete example of this oozone is found in Coll de Nargó Syncline, where these three oospecies occurred in a single stratigraphical level. More common are the associations between two of these three oospecies. (e.g. *M. siruguei* + *Cairanoolithus* have been reported from Corbieres, Villaveyrac and Rouquehautes Grand Creux sections; *M. aureliensis* + *Cairanoolithus* association is present in La Cairenne site; and *M. siruguei* + *M. aureliensis* combination was found in Villaveyrac site; see Garcia and Vianey-Liaud, 2001b). In the Àger and Tremp basins, this oozone is represented only by *M. aureliensis* in Blancafort (in this thesis) and Fontllonga-6 site (Vianey-Liaud and López-Martínez, 1997). To date, this oozone has not been reported from the Vallcebre Syncline (see Vila *et al*., 2011), neither from Romania.

M. aureliensis oozone differs from the formal definition of Assemblage 1 of Garcia and Vianey-Liaud (2001b) in the absence of *M. microtuberculata* and *M. petralta,* both considered junior synonymous of *M. siruguei* and *M aureliensis*, respectively (see chapeter 4.1.2).

According to French authors, this lower egg-assemblage was restricted to the Late Campanian, ranging from the chrone C33 to chrone C32, and finishing with the last occurrence of *Cairanoolithus* oogenus. However, based in new data from south-central Pyrenees, this event coincides with the last occurrence of *M. aureliensis.*

The youngest site containing the *Megaloolithus aureliensis* + *Cairanoolithus* oozone is considered “El Mirador” level in the Coll de Nargó Syncline. No chronostratrigraphical data has been provided for this site, and studies on charophytes assemblages from this area do not offered significant information (Feist and Colombo, 1983). Based on stratigraphical criteria (Riera, 2010), we could consider “El Mirador” level equivalent to the middle-upper part of the Grey unit in Vallcebre Syncline, which has been dated in the transition between C32n.1n and C31r magnetozones (Vila *et al*., 2011). This result is confident with those obtained for the same oozone in South France (e.g. Albas section, see Garcia and Vianey-Liaud, 2001b, fig. 3b, 4).

Other ootaxa related to this oozone should be *Prismatoolithus matellensis* and *Prismatoolithus tenuis* because both oospecies are restricted to the Campanian, and sometimes co-occurring with *M. aureliensis* in the same site, as occurred in Fontllonga-6 (Vianey-Liaud and López-Martínez, 1997) or in the Rousset-Erben section (Garcia and Vianey-Liaud, 2001b).

2) *Megaloolithus siruguei* oozone: This oozone is represented by the only possible occurrence of *M. siruguei.* This oospecies is the most common *Megaloolithus* oospecies in Europe, being reported from many sites of Spain (Moratalla, 1993; Izquierdo *et al*., 1999; Bravo *et al*., 2005; Escuer *et al*., 2006; Company *et al*., 2009, Vila *et al*., 2010c, 2011; among others), France (Vianey-Liaud *et al*., 1994; Garcia, 1998; Garcia and Vianey-Liaud, 2001a,b; among others) and Romania (Grigorescu *et al*., 1990, Codrea *et al*., 2002; Garcia *et al*., 2002, 2009; Grigorescu and Csiki, 2008, among others). The absence of precise dating of many of these sites does not allow use them in our biostratigraphical study.

As it was previously mentioned, *Megaloolithus siruguei* oozone replaces the Assemblage 2 of Garcia and Vianey-Liaud (2001b). The base of this oozone is marked by the last occurrence of both *Cairanoolithus* and *M. aureliensis* at the beginning of the C31r, and its top is characterized by the first occurrence of the oospecies *Megaloolithus mamillare*, according to Vila *et al*. (2011). This event has been established in the transitions between chrone C31r and C31n. The top of *Megaloolithus siruguei* oozone is not reported in the Coll de Nargó Syncline, because the absence of *M. mamillare*. In the same way, it not was possible delimit this oozone in the Àger and Tremp basins, because sites yielding *M. siruguei* (Biscarri, Barranc de la Fonguera and Coll de Faidella) have not been dated and stratigraphic correlations were not possible.

Romanian Fossil sites-bearing megaloolithid eggs and eggshells could be tentatively referred to *Megaloolithus siruguei* oozone (Fig. 35C) by following characters: *Megaloolithus siruguei* is the unique oospecies found in the oological record of Upper Cretaceous of Romania (Grigorescu *et al*., 1990; Garcia *et al*., 2002, 2003, 2009; Grigorescu and Csiki, 2008, among others). Only two geological formation yielding oological remains in Romania. In one hand, magnetostratigraphic works conducted by Panaiotu and Panaiotu (2010) in the Sânpetru Fm. reveals that this formation range from the chrone C32n.1n (Late Campanian) to the base of chrone C30r (Late Maastrichtian); while the Densuş-Ciula Fm. is considered as Maastrichtian in age (Pătraşcu *et al*., 1992).

3) *Megaloolithus mamillare* + *Megaloolithus baghensis* oozone: The youngest megaloolithid eggs assemblage is characterized by the possible co-occurrence of *M. mamillare* and *M .baghensis*. Indeed, this co-occurrence has been reported only in one site of south France (Rousset-Erben La Cairenne section; see Garcia and Vianey-Liaud, 2001b, fig. 3A) and in tree sites of South Pyrenees (Torrent de l'Esdavella, Suterranya, Orcau and l'Abeller, see Fig. 33, 38A), but frequently each site yields only one oospecies of *Megaloolithus*.

The *Megaloolithus mamillare* + *Megaloolithus baghensis* is considered equivalent to Assemblge 3 of Garcia and Vianey-Liaud (2001b) and, according to new information provided by Vila *et al*. (2011), the base of this oozone is marked by the last occurrence of *M. siruguei* in the chrone C31r.

Apparently, *M. mamillare* appears first than *M. baghensis*. In Southern Pyrenees, oldest remains of *M. mamillare* are located at El Terrers section in Vallcebre Syncline (see Vila *et al*., 2011). In this site, *M. mamillare* co-occurred together with *M. siruguei* in the transition between chrones C31r and C31n, like in Provence region. On the other hand, first apparition of *M. bagensis* in south-central Pyrenees could be attributed to specimens from Coll de Nargó Syncline, but the absence of confident dating does not allow confirm this hypothesis. Stratigraphically, the next remain attributed to *M. baghensis* appears at L'Espinau site (Tremp Baisn). Not dating is reported from L'Espinau site, but according to its stratigraphical position it could be placed in the Chrone C31n (see Fig. 34). This interpretation differs slightly from the magnetostratigraphical dating for *M. bagensis* in southwestern France, where the first apparition of this ootaxa is established near the base of Chrone C30n (Garcia and Vianey-Liaud, 2001b, Fig. 3B, 4B).

Concerning the last occurrence of *M. mamillare*, the last specimens of this oospecies in south-central Pyrenees are located in the Tossal de Sant Romà site (Tremp Basin), which is dated as in chrone C30n (Riera *et al*., 2009); while last *M. mamillare* from France occurs between chornes C30n and C29r in the East Arc Basin (see Garcia and Vianey-Liaud, 2001b, Fig. 4B). According to that observation, *M. mamillare* would disappear at the same time that *M. baghensis*, but this interpretation seems do not agree with oological successions reported in the same work (see Garcia and Vianey-Liaud, 2001b). But frequently, *M. mamillare* disappears from the fossil record some meters below the last occurrence of *M. baghensis*. The same appreciation can be observed in southern Pyrenees, where the last occurrence of *M. baghensis* (? C29r, Camí del Soldat) takes place several meter over the last apparition of *M. mamillare* (C30n, Tossal de Sant Romà).

Considering the last presence of megaloolithid eggs in the fossil record, it occurs between 10 to 20 meters below the K/Pg boundary in France (Garcia and Vianey-Liaud, 2001b). This last specimen occurs near the limit between C30n-C29r magnetochrone, meaning that the last *Megaloolithus* in France toke place 0.3 My before the K/Pg boundary. In its turn, the youngest *Megaloolithus* in South-Central Pyrenees it is located in the Camí del Soldat site, whose age has been inferred within the chrone C29r, probably 0.2 My before the K/Pg boundary. It could means that this last specimen represents the youngest *Megaloolithus* in Europe.

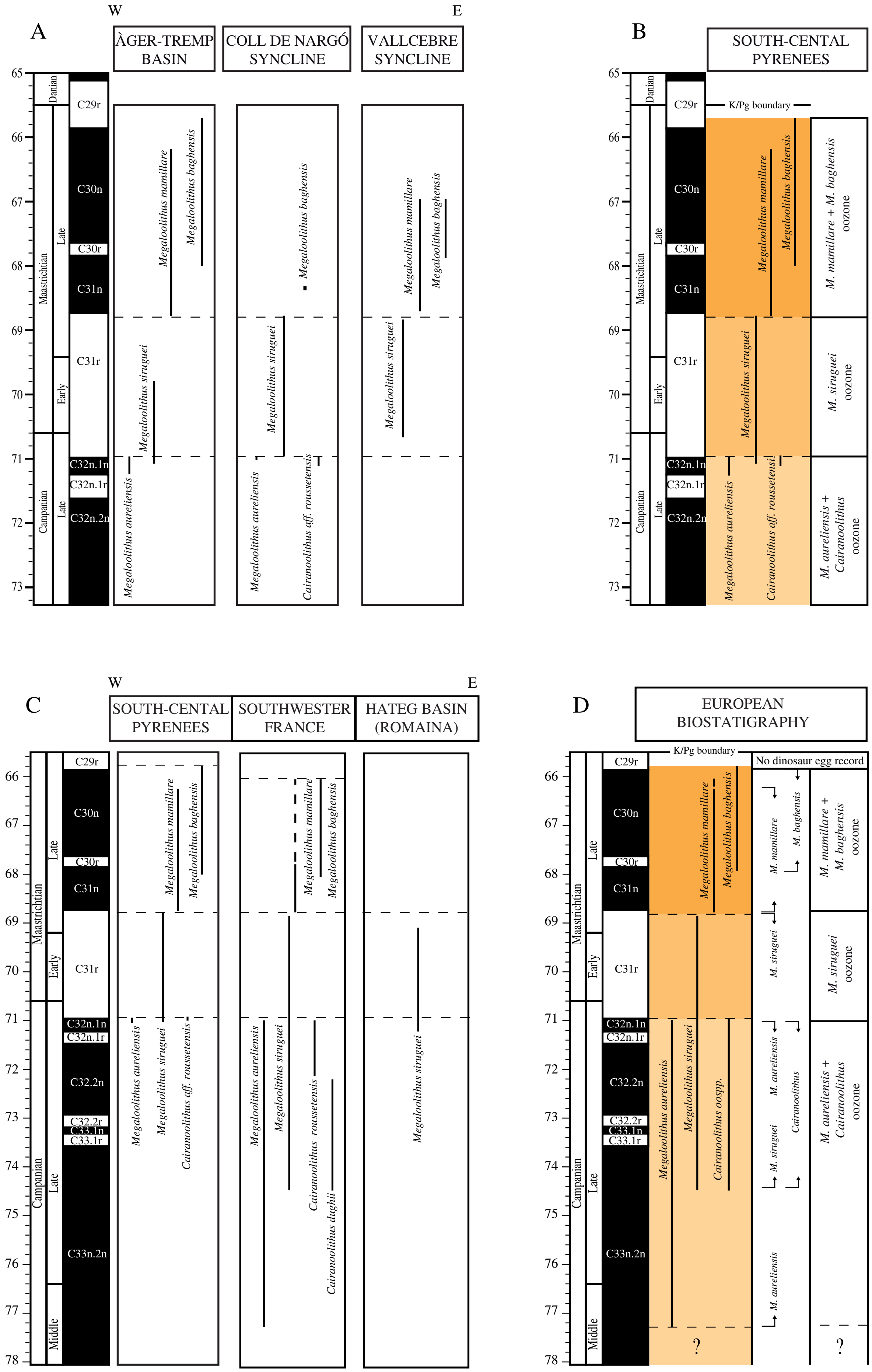

Figure 395 General biostratigraphy based on *Megaloolithus* succession . A) Comparison between South Pyreneean basins. B) General biostratigraphy for Southern Pyrenees. C) Comparison between European regions. D) General biostratigraphy based on *Megaloolithus* succession for South Europe showing the temporal distribution of each oozone and FAT and LAT of each oospecies.

GENERAL CONCLUSIONS

General Conclusions

The pluridisciplinary study of oological fossil remains attributed to dinosaurs in the Upper Cretaceous of Southern Pyrenees has provided new data on systematics, phylogeny, diversity and biostratigraphy. Special attention was paid on megaloolithid eggs, as most of the studies presented here deepen on our knowledge of this group of fossil eggs.

As a first step, the global review of sauropod egg record and parataxonomical criteria used to distinguish and describe it allowed to obtain a general framework about this group of fossil eggs. More important, an update of this topic implied a significant reduction in the number of oospecies attributed to Megaloolithidae. Taking in consideration those results, the second step was to describe and determinate the oological diversity in the Upper Cretaceous of Southern Pyrenees and relate it to environmental factors, reproductive behaviors and its possible producing faunas. As a final step, biostratigraphical studies have been performed, updating the extant European megaloolithid biostratigraphy.

The general conclusions of this PhD thesis have been summarized in three parts in order to expose the results of the different chapters.

Systematic, problematic and phylogeny of dinosaur fossil eggs from the Late Cretaceous of Southern Pyrenees, with special interest in those related with sauropod dinosaurs.

All the oological remains attributed to dinosaurs, including birds, recovered from the Upper Cretaceous of South-central Pyrenees have been treated in **Chapters 4** and **5**. Due to the great abundance of fossil remains attributed to the oofamilyMegaloolithidae, it has been thought to treat them individually in **Chapter 4**. On the other hand, oological remains not associated to that oofamilly have been described in **Chapter 5**.

As an introduction and general contextualization, **Chapter 4.1** offers a review of the global record of fossil eggs attributed to sauropodomorph dinosaurs, because this oological record is the most abundant in Southern Pyrenees. This review is, indeed, one of the most complete revisions on sauropod eggs ever done. This study has revealed that oological record attributed to sauropodomorph dinosaurs range from the Norian (Late Triassic) to the end-Cretaceous times, being represented in all continents excluding Australia and Antarctica. One of the most interesting obtained results is that oological record could be linked with some of the major events in sauropod biogeographical history.

The oofamily Megaloolithidae is one of the most abundant dinosaur egg-types of the Upper Cretaceous continental deposits in the world. In **Chapter 4.2** a revision of all ootaxa attributed to Megaloolithidae is made. The critical revision reveals that some previously considered structural characters (e.g. egg size and shape, shell thickness, and pore pattern) are not good diagnostic characters, because they are subjected to strong intraspecific variations. On the other hand, other characters (e.g. shell unit shape and fusion, ornamental pattern, pore canal system and mammillare size and density) could be good diagnostic characters for megaloolithids eggs. Based on the great similitude observed between different oospecies, three structural groups, grouping different oospecies from all over the world have been defined. Furthermore, this comparative study allows the reevaluation of previously described ootaxa. Summarizing, from the 20 former oospecies only 10 can be considered valid. Most of them have been synonymized to other, with the exception of *M. megadermus*, which is considered *nomen dubium*, and *Spheroolithus problematica*, considered a nov. com.

According with previous results, four valid megaloolithid ootaxa have been described from the Late Cretaceous of Catalonia (**Chapter 4.3**): *M. aureliensis*, *M. siruguei, M. mamillare* and *M. baghensis*.

An unexpected high diversity of oological material from the Late Cretaceous basins of Southern Pyrenees are described in **Chapter 5** and **6**. The first remains of *Cairanoolithus* oogenus (**Chapter 5.1**) recovered from outside France, which was considered an endemic egg type from that region, have provided new information on its eggshell structure, thus revealing significant differences with Megaloolithus, its supposed sister group. Given that, it was necessary to erect a new parataxonomical group (Cairanoolithidae nov. oofam.), for including this ootaxon. On its turn, new material is described in **Chapter 5.2**, including the first occurrences of *Spheroolithus* in Europe, which could represent a new ootaxon, and many different types of *Prismatoolithus*. This last oogenus is currently represented by almost six species, some of them representing new taxa. One of the samples has been attributed *to Ageroolithus*, which could be related to therapods or birds. Based on new material, the relation between *Pseudogecoolithus* and dinosaurs has been discussed, and reinterpreted as much more similar to those of extant lizards.

Phylogenetical analysis **(Chapter 6)** reveals interesting results. In one hand, three main groups of Megaloolithus can be recognized in the obtained phylogenetical trees (**Chapter 6.1**), some of them with great structural affinity to *Spheroolithus*. It is also interesting the result that suggests that *Faveoloolithus* could represent a high derived *Megaloolithus*. Concerning to phylogenetical position of *Cairanoolithus* (**Chapter 6.1)**, it appears as the sister group of *Spheroolithus* and *Ovaloolithus*, both related with hadrosaurs. However, eggshell of hadrosaur and sauropod share many structural characters. This can be interpreted as a possible evaluative convergence (homopolasy) related to environmental constraints or to the reproductive physiology of these animals. Another hypothesis could be that both sauropods and hadrosaurs eggs would retain ancestral features of archosaur eggs.

Oodiversity, external factors and taxonomical relationships

Some results of this section are preliminary, but they allow deepening the knowledge of dinosaur oofauna during the Late Cretaceous of Southern Europe.

It is pointed out that the current oological diversity of Southern Pyrenees is composed of 13 different oospecies related to dinosaurs (**Chapter 7**). This oodiversity is only equaled by those of France, while it is much lower in other sites of the world. Furthermore, it is noted that ootaxa diversity is not constant along time, being richer in the Campanian than in the Maastrichtian.

The significant and drastic decrease of the oodiversity near the Campanian-Maastrichtian boundary could be related with environmental changes in the nesting areas (e.g. climatic changes, preference of nesting area); because this event cannot be explained by a relation of presence/absence of each ootaxon with its laying dinosaurs.

The previously questioned consistence between the current *Megaloolithus* ootaxa diversity and sauropod fauna diversity during the Late Cretaceous in South Europe is also demonstrated. These results must be taken as an approach for evaluating the dinosaur diversity based in an indirect record, as corresponds to oological record. According to our discussion, *M. aureliensis* could be attributed to basal titanosaurs; *M. siruguei* is frequently associated to lithostrotian sauropods; and *M. mamillare* could tentatively belong to derived titanosaurs, such as saltasaurs. Even *M. baghensis* seems to be related with aeolosaurids, this relationship cannot be established in Europe.

Biostratigraphy and *Megaloolithus* oospecies succession in the Late Cretaceous of Southern Europe

In **Chapter 8**, the biostratigraphical distribution of Megaloolithus in Southern Pyrenean basins has been addressed. New information about oological succession in Coll de Nargó Syncline and Àger and Tremp basins has been provided. Finally, the European megaloolithid biostratigraphy is revised and updated.

A terminological mistake is dragged for a long time in biosatrtigraphical studies made in megaloolithid eggs. In this last chapter, the term “assemblages” is replaced by “Oozone”, because this last term is more accurate than the previous one.

The biostratigraphical study performed in Coll de Nargó Syncline reveals three different oozones, which allows inferring the age of this sites (Late Campanian to Early Late Maastrichtian). Similar studies have been addressed in Àger and Tremp basins, giving similar results. Thus, it is concluded that three oozones have been identified in Southern Pyrenean areas, being represented by four ootaxa of Megaloolithus (*M. aurelines, M. siruguei, M. mamillare* and *M. baghensi)* and one oospeceis of *Cairanoolithus*. Based on chronostratigraphical correlations, it is established that sites yielding megaloolithid eggs range from the Late Campanian to the end of the Maastrichtian.

The review and updating of the European megaloolithid biostratigraphy allowed to define three oozones, which can be recognized in North-eastern Iberian Peninsula, South France and Romania:

1) ***M. aureliensis* + *Cairanoolithus* oozone:** It is composed by the possible co-occurrence of *M. aureliensis*, *M. siruguei* and *Cairanoolithus* oogenus. The base of this oozone is unknown but its top is placed near the limit between C32n.12 and C31r, in the Late Campanian, with the LAT of *M. aureliensis* and *Cairanoolithus* oogenus.

2) ***M. sirugei* oozone:** It is characterized by the unique possible occurrence of *M. siruguei* oospecies. Its upper boundary is located near the magnetic change between Chrones C31r and C31n, in the Upper Maastrichtian. This limit is marked by the LAT of *M. siruguei* and the FAT of *M. mamillare*.

3) ***M. mamillare* + *M. baghensis* oozone**: It is defines by the possible co-occurrence of *M. mamillare* and *M. bagehnsis* oospecies. FAT of *M. mamillare* occurs near the C31r-C31n magnetic change, while FAT of *M. baghensis* is placer around the Chrone C30r. The upper limit of this oozone is established at the base of the Chrone C29r, few meters below the K-Pg boundary.

All this new information will help completing the fossil record of the continental Late Cretaceous of South-Central Pyrenees and understanding some behavior patterns of dinosaurs.

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APPENDICES

APPENDIX I

List of the material studied in this thesis.

REFERENCE	Nº SAMPLES	OOTAXA	LOCALITY
ISP-58945	1	*Faveoloolithus*	Rio Negro Prov. (Argentina)
ISP-58946	1	*Faveoloolithus*	Rio Negro Prov. (Argentina)
ISP-58947	2	*Faveoloolithus*	Rio Negro Prov. (Argentina)
ISP-58948	1	*Faveoloolithus*	La Pampa Prov. (Argentina)
ISP-58949	1	*Megaloolithus*	"Auca Mahuevo" site, Neuquén Prov. (Argentina)
ISP-58950	36	*Spheroolithus*	Level 1 of "Egg Mountain", Montana (USA)
ISP-58951	2	*Spheroolithus*	Level 2 of "Egg Mountain", Montana (USA)
ISP-58952	2	*Elongatoolithus*	"Egg Mountain", Montana (USA)
ISP-58953	6	*Elongatoolithus*	Nesting level of "Egg Mountain", Montana (USA)
ISP-58954	1	*Spheroolithus (S. maiasauroides)*	Unknown site, Inner Mongolia (China)
ISP-58955	4	*Megaloolithus (M. microtuberculata)*	La Cairanne, Aix-en Provence (France)
ISP-58956	4	*Cairanoolithus (C. dughii)*	La Cairanne, Aix-en Provence (France)
ISP-58957	1	*Megaloolithus (M. siruguei)*	La Begude, Aix-en Provence (France)
ISP-58958	2	*Cairanoolithus (C. roussetensis)*	Argelier (France)
ISP-58959	15	*Megaloolithus (M. aureliensis)*	Blancafort, Lleida Prov. (Spain)
ISP-58960	90	*Megaloolithus (M. cf. baghensis)*	Barranc de la Boiga, Lleida Prov. (Spain)
ISP-58961	2	*? Prismatoolithus*	Barranc de la Boiga , Lleida Prov. (Spain)
ISP-58962	3	*Prismatoolithus cf. tenuis*	Barranc de la Boiga , Lleida Prov. (Spain)
ISP-58963	101	*Megaloolithus (M. mamillare)*	Tossal de St. Romá , Lleida Prov. (Spain)
ISP-58964	109	*Megaloolithus (M. mamillare)*	Costa de la Coma , Lleida Prov. (Spain)
ISP-58965	36	*Megaloolithus (M. mamillare)*	Els Nerets , Lleida Prov. (Spain)
ISP-58966	102	*Megaloolithus (M.siruguei)*	Coll de la Faidella , Lleida Prov.

			(Spain)
ISP-58967	10	*Megaloolithus (M. cf. baghensis)*	Abella , Lleida Prov. (Spain)
ISP-58968	17	*Megaloolithus (M. cf. baghensis)*	Suterranya , Lleida Prov. (Spain)
ISP-58969	2	*Krokolithes*	Serrat del Pelleu, Lleida Prov. (Spain)
ISP-58970	150	*?Pseudogeckoolithus*	Serrat del Pelleu, Lleida Prov. (Spain)
ISP-58971	68	*Pseudogeckoolithus nodosus*	Serrat del Pelleu, Lleida Prov. (Spain)
ISP-58973	21	*Spheroolithus*	Pont d'Orrit , Lleida Prov. (Spain)
ISP-58974	200	*Mixed*	Moli del Baró, Lleida Prov. (Spain)
ISP-58975	50	*Megaloolithus (M. cf. baghensis)*	Moli del Baró, Lleida Prov. (Spain)
ISP-58976	150	*Prismatoolithus cf. tenuis*	Moli del Baró, Lleida Prov. (Spain)
ISP-58977	500	*Pseudogeckoolithus nodosus*	Moli del Baró, Lleida Prov. (Spain)
ISP-58978	8	*Prismatoolithus cf. tenuis*	Basturs poble, Lleida Prov. (Spain)
ISP-58979	27	*indet*	Serrant del Rostià-Maxila, Lleida Prov. (Spain)
ISP-58980	100	*Pseudogeckoolithus nodosus*	Serrant del Rostià-Maxila, Lleida Prov. (Spain)
ISP-58981	103	*? Krokolithes*	Serrant del Rostià-Maxila, Lleida Prov. (Spain)
ISP-58982	1	*Megaloolithus (M. cf. baghensis)*	Serrant del Rostià-Maxila, Lleida Prov. (Spain)
ISP-58983	17	*Prismatoolithus tenuis*	Serrant del Rostià-Maxila, Lleida Prov. (Spain)
ISP-58984	80	*indet*	Camí del Soldat, Lleida Prov. (Spain)
ISP-58985	28	*Prismatoolithus tenuis*	Camí del Soldat, Lleida Prov. (Spain)
ISP-58986	16	*Pseudogeckoolithus nodosus*	Camí del Soldat, Lleida Prov. (Spain)
ISP-58987	50	*Megaloolithus (? M. cf. baghensis)*	Camí del Soldat, Lleida Prov. (Spain)
ISP-58972	1	*Elongatoolithus/Ratites*	L'Espinau, Lleida Prov. (Spain)
ISP-58988	80	*Mixed*	L'Espinau, Lleida Prov. (Spain)
ISP-58989	60	*Pseudogeckoolithus nodosus*	L'Espinau, Lleida Prov. (Spain)
ISP-58990	25	*Prismatoolithus tenuis*	L'Espinau, Lleida Prov. (Spain)
ISP-58991	3	*? Krokolithes*	L'Espinau, Lleida Prov. (Spain)

ISP-58992	8	*Megaloolithus (? M. cf. baghensis)*	L'Espinau, Lleida Prov. (Spain)
ISP-58993	59	*Pseudogeckoolithus nodosus*	L'Espinau, Lleida Prov. (Spain)
ISP-58994	9	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-58995	4	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-58996	6	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-58997	6	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-58998	6	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-58999	6	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59000	4	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59001	4	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59002	4	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59003	16	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59004	7	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59005	9	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59006	6	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59007	6	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59008	6	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59009	6	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59010	7	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59011	5	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)

ISP-59012	4	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59013	7	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59014	14	*Megaloolithus (M.cf. baghensis)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59015	25	*Cairanoolithus (C. roussetensis)*	"El Mirador" level in Pinyes site, Lleida Prov. (Spain)
ISP-59016	10	*Cairanoolithus (C. roussetensis)*	"El Mirador" level in Pinyes site, Lleida Prov. (Spain)
ISP-59017	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59018	4	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59019	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59020	1	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59021	6	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59022	1	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59023	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59024	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59025	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59026	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59027	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59028	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59030	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59031	5	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)

ISP-59032	4	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59033	1	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59034	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59035	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59036	8	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59037	5	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59038	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59039	6	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59040	1	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59041	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59042	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59043	5	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59044	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59045	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59046	1	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59047	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59048	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59049	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)
ISP-59050	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 190), Coll de Nargó, Lleida Prov. (Spain)

ISP-59051	4	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59052	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59053	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59054	5	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59055	4	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59056	7	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59057	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59058	7	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59059	5	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59060	8	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59061	7	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59062	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59063	4	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59064	4	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59065	5	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59066	4	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59067	7	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59068	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59069	4	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)

ISP-59070	9	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59071	5	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59072	9	*Megaloolithus (M. siruguei)*	Pinyes (cota 198), Coll de Nargó, Lleida Prov. (Spain)
ISP-59073	18	*Cairanoolithus (C. roussetensis)*	“El Mirador” level in Pinyes site, Lleida Prov. (Spain)
ISP-59074	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59075	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59076	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59077	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59078	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59079	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59080	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59081	4	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59082	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59083	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59084	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59085	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59086	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59087	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59088	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)

ISP-59089	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59090	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59091	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59092	1	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59093	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59094	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59095	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59096	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59097	4	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59098	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59099	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59100	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59101	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59102	2	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59103	3	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59104	4	*Megaloolithus (M. siruguei)*	Pinyes (cota 22), Coll de Nargó, Lleida Prov. (Spain)
ISP-59105	17	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59106	63	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59107	10	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)

ISP-59108	55	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59109	19	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59110	18	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59111	3	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59112	2	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59113	105	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59114	24	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
ISP-59115	35	*Megaloolithus (M. siruguei)*	Pinyes, Coll de Nargó, Lleida Prov. (Spain)
1A01	1	*Prismatoolithud* sp. Indet.	La Massana outcrop, La Noguera, Lleida Prov. (Spain)
1A04	1	*Prismatoolithud* sp. Indet.	La Massana outcrop, La Noguera, Lleida Prov. (Spain)
1A06	1	*Prismatoolithud* sp. Indet.	La Massana outcrop, La Noguera, Lleida Prov. (Spain)
1A07	1	*Prismatoolithud* nov. oosp.	La Massana outcrop, La Noguera, Lleida Prov. (Spain)
1B01	1	*Prismatoolithud* cf. *levis* + cf. *Ageroolithus*	La Massana outcrop, La Noguera, Lleida Prov. (Spain)
1B04	1	cf. *Ageroolithus*	La Massana outcrop, La Noguera, Lleida Prov. (Spain)
7B03	1	*Prismatoolithud* sp. Indet.	La Massana outcrop, La Noguera, Lleida Prov. (Spain)
7B05	1	*Prismatoolithud* sp. Indet.	La Massana outcrop, La Noguera, Lleida Prov. (Spain)

APPENDIX II

APPENDIX II.1. List of egg and eggshell characters used in phylogenetic analysis of *Megaloolithus* oospecies.

1. Eggshell, composition: aragonite (0); calcite (1) [ordered].
2. Eggshell, nucleation centers, spacing relative to shell width: >0.40 (0); 0.33–0.40 (1); 0.24–0.33 (2); <0.24 (3) [ordered].
3. Eggshell, nucleation centers: at base of mammillary layer (0), within layer (1) [unordered].
4. Eggshell, mammillary layer, composition: crystalline (0); organic and crystalline (1) [unordered].
5. Eggshell, mammillary layer, radiating crystal form: acicular (0); wedge-like (1); bladed-like (2); tabular (3) [unordered].
6. Eggshell, transition between first and second structural layers: abrupt (0); gradual (1) [unordered].
7. Eggshell, second layer: absent (0); prismatic (1); wedge (2) [ordered].
8. Eggshell, second layer, squamatic structure: absent (0); present (1) [ordered].
9. Eggshell, second layer, squamatic structure type: regular, masks prisms (0); evenly distributed, visible prisms (1); irregular, prisms visible (2) [unordered].
10. Eggshell, second layer, book-like horizontal laminations: absent (0); present (1) [unordered].
11. Eggshell, transition between second and third structural layers: gradual (0); abrupt (1) [unordered].
12. Eggshell, third layer: absent (0); present (1) [ordered].
13. Eggshell, third layer, structure: horizontal crystals (0); vertical crystals (1); with porous and crystalline regions (2) [unordered].
14. Eggshell, pore system: straight with consistent width (0); straight with enlarged base (1); straight to oblique (2); irregular and varying (3); branched (4); reticulate (5) [ordered].
15. Eggshell, cuticle: absent (0); present (1) [ordered].
16. Eggshell, ornamentation: smooth (0); with ridges (1); coalescent nodes (2); nodular (3) [ordered].
17. Eggshell, fused shell units: absent (0); partially (1); completely (2) [ordered].
18. Eggshell, shell units shape: short fan-shape (0); slender fan-shape (1); irregular fan-shape (2); prismatic (3) [unordered].
19. Eggshell, thickness: $0 \leq X \leq 1$ (0); $1.1 \leq X \leq 2$ (1); $2.1 \leq X \leq 3$ (2); $X \geq 3$ (3) [unordered].
20. Egg, shape: symmetrical (0); asymmetrical (1) [ordered].
21. Egg, size, relative to adult body size: small, <0.10 Eb (0); medium, 0.10–0.30 Eb (1); large, >0.30 Eb (2) [ordered]. Eb is the mass of an egg predicted for a bird of similar adult size using an allometric equation based on modern data (Blueweiss et al., 1978) [ordered].
22. Clutch, arrangement: random/massed (0); eggs paired (1); open, one layer (2) [unordered].

APPENDIX II.2. Data matrix for characters used for phylogenetic analysis.

TAXA	OOTAXA	1-5	6-10	11-15	16-20	21-22
Melanochelys trijuga	-	000??	?0???	?0?00	0000	020
Malacochersus tornieri	-	000??	?0???	?0?00	0000	020
Rhinoclemmys areolata	-	000??	?0???	?0?10	0000	020
Alligator mississippiensis	-	10111	120?1	01011	0000	000
Crocodylus niloticus	-	10111	120?1	01011	0000	000
Maiasaura	*Spheroolithus*	11000	?0???	?0?3?	1131	000
?Ornithopod	*Sheroolithus problematica*	11000	?0???	?0?3?	1131	000
Sauropod (Titanosauria)	*M. dholiyaensis*	11000	?0???	?0?0?	2131	000
	M. jabalpurensis	11000	?0???	?0?0?	3002	000
	M. mamillare	11000	?0???	?0?0?	3001	000
	M. baghensis	11000	?0???	?0?2?	2121	000
	M. aureliensis	11000	?0???	?0?0?	3120	000
	M. siruguei	11000	?0???	?0?5?	3012	000
	M. cylindricus	11000	?0???	?0?0?	3012	000
	M. mohabeyi	11000	?0???	?0?0?	3011	000
	M. khempurensis	11000	?0???	?0?5?	3012	000
	M. maghrebiensis	11000	?0???	?0?3?	2122	000
?Sauropod	*Faveoloolithus*	11000	?0???	?0?4?	3013	000
Troodon formosus	*Prismatoolithus*	13002	11121	0110?	0241	121
Oviraptorid	*Elongatoolithus*	13001	0?101	10?0?	1241	?21
Large theropod	*Macroelongatoolithus*	13001	01101	10?0?	1241	??1
Cretaceous bird	unnamed	1300?	11110	01101	0240	1??
Struthio sp.	-	13001	01111	01141	0242	122
Gallus gallus	-	12002	11111	01101	0240	122

APPENDIX III

APPENDIX III.1. List of egg and eggshell characters used in phylogenetic analysis of *Cairanoolithus*.

1. Eggshell, composition: aragonite (0); calcite (1) [ordered].
2. Eggshell, nucleation centers, spacing relative to shell width: >0.40 (0); 0.33–0.40 (1); 0.24–0.33 (2); <0.24 (3) [ordered].
3. Eggshell, nucleation centers: at base of mammillary layer (0), within layer (1) [unordered].
4. Eggshell, mammillary layer, composition: crystalline (0); organic and crystalline (1) [unordered].
5. Eggshell, mammillary layer, radiating crystal form: acicular (0); wedge-like (1); bladed-like (2); tabular (3) [unordered].
6. Eggshell, transition between first and second structural layers: abrupt (0); gradual (1) [unordered].
7. Eggshell, second layer: absent (0); prismatic (1); wedge (2) [ordered].
8. Eggshell, second layer, squamatic structure: absent (0); present (1) [ordered].
9. Eggshell, second layer, squamatic structure type: regular, masks prisms (0); evenly distributed, visible prisms (1); irregular, prisms visible (2) [unordered].
10. Eggshell, second layer, book-like horizontal laminations: absent (0); present (1) [unordered].
11. Eggshell, transition between second and third structural layers: gradual (0); abrupt (1) [unordered].
12. Eggshell, third layer: absent (0); present (1) [ordered].
13. Eggshell, third layer, structure: horizontal crystals (0); vertical crystals (1); with porous and crystalline regions (2) [unordered].
14. Eggshell, pore system: straight with consistent width (0); straight with enlarged base (1); straight to oblique (2); irregular and varying (3); branched (4); reticulate (5) [ordered].
15. Eggshell, cuticle: absent (0); present (1) [ordered].
16. Eggshell, ornamentation: smooth (0); with ridges (1); with ridges and nodes (2); nodular (3) [ordered].
17. Egg, shape: symmetrical (0); asymmetrical (1) [ordered].
18. Egg, size, relative to adult body size: small, <0.10 Eb (0); medium, 0.10–0.30 Eb (1); large, >0.30 Eb (2) [ordered]. Eb is themass of an egg predicted for a bird of similar adult size using an allometric equation based on modern data (Blueweiss et al., 1978) [ordered].
19. Clutch, arrangement: random/massed (0); eggs paired (1); open, one layer (2) [unordered].
20. Eggshell, fused shell units: absent (0); partially (1); completely (2) [ordered].

APPENDIX III.2. Data matrix for characters used for phylogenetic analysis.

Melanochelys trijuga		000??	?0???	?0?00	00200
Malacochersus tornieri		000??	?0???	?0?00	00200
Rhinoclemmys areolata		010??	?0???	?0?10	00200
Alligator mississippiensis		10111	120?1	01011	00000
Crocodylus niloticus		10111	120?1	01011	00000
Maiasaura	*Spheroolithus*	11000	?0???	?0?3?	20001
Ornithopod	*Ovaloolithus*	11000	?0???	?0?1?	20001
?	*Cairanoolithus*	11000	?0???	?0?2?	20?01
Titanosaur	*Megaloolithus*	11000	?0???	?0?0?	30000
?Sauropod	*Faveoloolithus*	11000	?0???	?0?4?	30000
? Theropod	*Dictyoolithus hongpoensis*	13001	010?1	?0?5?	00?02
Lourinhanosaurus	*cf. Preprismatoolithus*	12002	11121	0112?	11102
Troodon formosus	*Prismatoolithus*	13002	11121	0110?	01212
Therizinosaurid	*Dendroolithus*	12001	?1120	???5?	10002
Oviraptorid	*Elongatoolithus*	13001	0?101	?0?0?	1?212
Deinonychus	*cf. Elongatoolithus*	13001	01101	?0???	1???2
Large theropod	*Macroelongatoolithus*	13001	01101	?0?0?	1??12
Two Medicine Formation egg	unnamed	13002	11121	11201	10?12
Cretaceous bird	unnamed	1300?	11110	01101	01??2
Struthio sp.		13001	01111	01141	01222
Gallus gallus		12002	11111	01101	01222

“...I tu, nerviosa, com sempre que et toca ser en centre d'atenció,
has fixat els ulls en un punt imprecís del mejador.
Un segón, dos segons, tres segons, quatre... i cinc.”

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