

# DIVERSITY AMONG NORTH AFRICAN DINOSAUR EGGSHELLS

by

Monique VIANEY-LIAUD\* and Géraldine GARCIA\*\*

## SUMMARY

	Page
Abstract, Résumé .....	172
Introduction .....	172
Material and methods .....	173
Eggshells systematics .....	173
Oofamily Megaoolithidae ZHAO, 1975 .....	173
Oofamily ? Elongatoolithidae ZHAO, 1975 .....	179
Oofamily ? Subtiliolithidae MIKHAÏLOV, 1991 .....	182
Oofamily ? Prismatoolithidae HIRSCH, 1994 .....	183
Discussion and conclusion .....	184
Acknowledgements .....	185
References .....	185
Captions of the plates .....	187

\* Institut des Sciences de l'Evolution, Université Montpellier II, Place Eugène Bataillon, 34095 Montpellier cedex 05, France.

\*\* Laboratoire de Géobiologie, Biochronologie et Paléontologie Humaine, UMR 6046, Université de Poitiers, 40 Avenue du Recteur Pineau, 86022 Poitiers cedex, France.

**Mots-clés:** Diversité des dinosaures; coquilles d'œufs : taxonomie; Afrique du Nord ; Maroc; Crétacé; Maastrichtien

**Key-words:** Dinosaurs diversity; Eggshells: taxonomy; North Africa; Morocco; Cretaceous; Maastrichtian

*Palaeovertebrata*, Montpellier, 32 (2-4): 171–188, 6 fig., 5 tabl., 6 pl.

(Reçu le 15 Octobre 2003, accepté le 15 Novembre 2003, publié le 15 Décembre 2003)

## ABSTRACT

Until the discovery of dinosaur eggshells locality in the Oukdiksou syncline, (Middle Atlas, Morocco) in 1999 (Garcia *et al.* this volume) the maastrichtian reptiles faunas were unknown in North Africa. Additional material from Achloulj-2 allows us to describe five oospecies, belonging to four oofamilies. The Megaloolithidae is recorded by *Megaloolithus maghrebiensis* GARCIA *et al.* and *Pseudomegaloolithus atlasi* oogen. nov. oospec. nov. *Tipoolithus achlouljensis* GARCIA *et al.* is questionably considered as a Subtiliolithidae. A relatively small Elongatoolithidae is represented by *Rodolphoolithus arioul* oogen. nov. oospec. nov. A thin Prismatoolithidae is described as a new oospecies of ? *Pseudogeckoolithus* VIANEY-LIAUD & LOPEZ-MARTINEZ, 1997: *P. tirboulensis*. The diversity of these oospecies indicates that the dinosaur fauna comprises at least five dinosaur oospecies, with perhaps one sauropod and three theropods.

## RESUME

On ne connaissait pas de faune dinosaurienne bien repérée stratigraphiquement dans le Maastrichtien supérieur d'Afrique jusqu'à la découverte des localités fossilifères du synclinal d'Oukdiksou (Moyen Atlas, Maroc) en 1999 (Garcia *et al.*). L'exploitation systématique de la section d'Achloulj-2 a livré de nombreux fragments de coquilles d'oeufs de dinosaures permettant de décrire ici cinq oospèces appartenant à quatre oofamilles. Les Megaloolithidae sont documentés par *Megaloolithus maghrebiensis* GARCIA *et al.*, et *Pseudomegaloolithus atlasi* oogen. nov. oospec. nov. *Tipoolithus achlouljensis* GARCIA *et al.* est attribué avec doute aux Subtiliolithidae. Un Elongatoolithidae relativement petit et mince est nommé *Rodolphoolithus arioul* oogen. nov. oospec. nov. . Un Prismatoolithidae à coquille mince est décrit comme une nouvelle oospèce attribuée avec doute à l'oogénre *Pseudogeckoolithus* VIANEY-LIAUD & LOPEZ-MARTINEZ, 1997: *P. tirboulensis*. La diversité de ces oospèces permet de supposer que la faune dinosaurienne comprenait au moins cinq espèces dont peut être un sauropode et trois théropodes .

## INTRODUCTION

For the first time in Africa, we have reported dinosaur eggshells from upper Maastrichtian deposits (Garcia *et al.*, this volume). During a prospection for early tertiary mammals in Central Morocco, in 1999, R. Tabuce and B. Marandat have found a few fragments of tuberculate eggshells in fluvial deposits. Several field campaigns followed this discovery, and several outcrops which straddle the Maastrichtian/Paleocene transition have been sampled. Extensive excavations in the Oukdiksou syncline (Middle Atlas), through the Achloulj section (Achloulj 2, level 16 to 19) significantly increased the number of eggshells fragments. Even if, because of the fluvial origins of the sediments, no complete egg has been found, new material and new oospecies can be now described. They are referred at least to 4 oofamilies. The Megaloolithidae are documented by 2 oospecies and the three others (Elongatoolithidae, Subtiliolithidae, Prismatoolithidae ) by one oospecies.

## MATERIAL AND METHODS

The sediment resulting of the excavations has been carried out and six hundred kilos have been processed in Montpellier II University. The eggshells have been prepared by ultrasonic cleaning, and some, as they were strongly incrustated, by acetic acid (5%) processing. Fragments and thin sections have been measured under a Nikon mesuroscope. They have been studied in thin sections and SEM preparations.

We provide figures of eggshells fragments without preparation, except cleaning, drawn with the camera lucida of a Leica-Wild binocular microscope, as well as pictures of thin sections (25 µm), or SEM pictures made either on polished or naturally broken sections. Numerous illustrations combined with the descriptions contribute to give a better idea of the variability of the arrangements of the units and pore-system.

The terminology follows that of Mikhaïlov (1991, 1997), Hirsch (1994) and Mikhaïlov *et al.* (1996) but we use the " structural morphotypes " only as characters, for the description and diagnosis of the oofamily, oogenus and ospecies ranks.

## EGGSHELLS SYSTEMATICS

Oofamily: *MEGALLOOLITHIDAE* ZHAO, 1975 (emend. 1979)

**Definition of the oofamily:** (from Garcia & Vianey-Liaud, 2001)

Growth units generally discrete, scarcely fused; pore canals transverse to oblique, generally separated, but sometimes linked by oblique bridges; external surface generally compactituberculate with some scarce flat areas; growth lines generally semi-concentric, more or less convex: eggshell thickness 0.7 to 3.8 mm; big spherical or oval eggs (150 to 250 mm in diameter)

Oogenus: *MEGALLOOLITHUS* VIANEY-LIAUD *et al.*, 1994

**Definition:** as for the family, and generally fan-shaped units, with prominent nodes on the outer surfaces.

*Megaloolithus maghrebiensis* GARCIA *et al.*, 2004

(Plate 1 a to f, Plate 2 a to c, figures 1-2)

**Diagnosis :** cf. Garcia *et al.*, this volume.

**Localities:** Achlouj 2, levels 17 to 19, in grey clays; Saf 1, in grey clays; middle Atlas, Morocco; Upper Maastrichtian

**Measurements and statistics:**

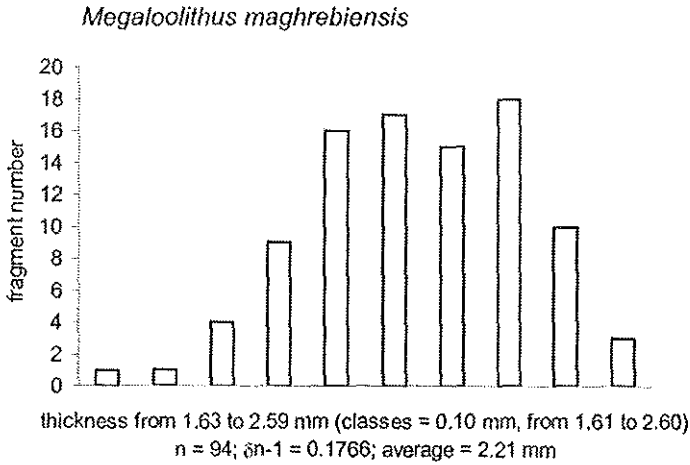


Table 1.— Measurements and statistics of *Megaloolithus maghrebiensis* from Achlouj2.

**Description and discussion**

*Megaloolithus maghrebiensis* is the most common in the localities, with about two hundred fragments in Achlouj 2 section, but also from several sections, all around the Oukdiksou syncline. It is irregularly compactituberculate, with nodes diameters varying from 0.5 to 1.3 mm. The units are fan shaped, with growth lines always arched in the mamillae, when the units are well distinct. Sometime flat areas correspond to fused units, where the growth lines continue from one to the other. Eggshell thickness vary generally from 1.86 to 2.59 mm (average = 2.21). Two thinner fragments are strongly worn.

Pore canals can be straight, or linked by oblique bridges, like in the European *M. siruguei*. The node diameters, are generally larger, and the units are more fan shaped, and the pore canals wider than in *M. siruguei*. Among the Indian oospecies, *M. mohabeyi* displays the closest microstructure, but the node diameters seems smaller, and the eggshell thinner. The units of the South American *Megaloolithus* are thinner and clearly less elongated.

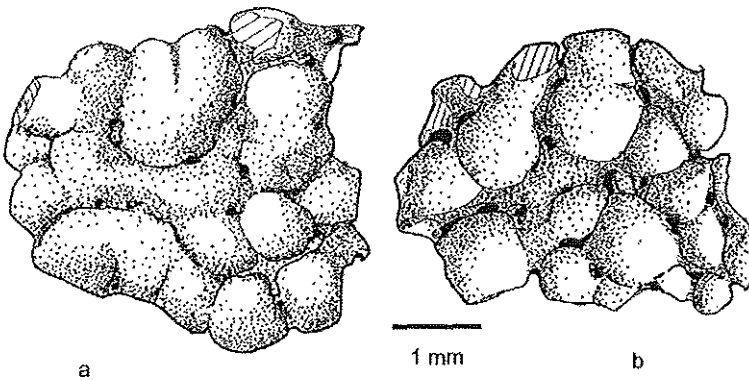


Figure 1.— Outer surface of two eggshells fragments of *Megaloolithus maghrebiensis* GARCIA *et al.* (this volume), from Achlouj 2 locality, level 18-19 (Middle Atlas, Morocco) showing the pore pattern around the nodes. a: ACH2-370; b: ACH2-371.

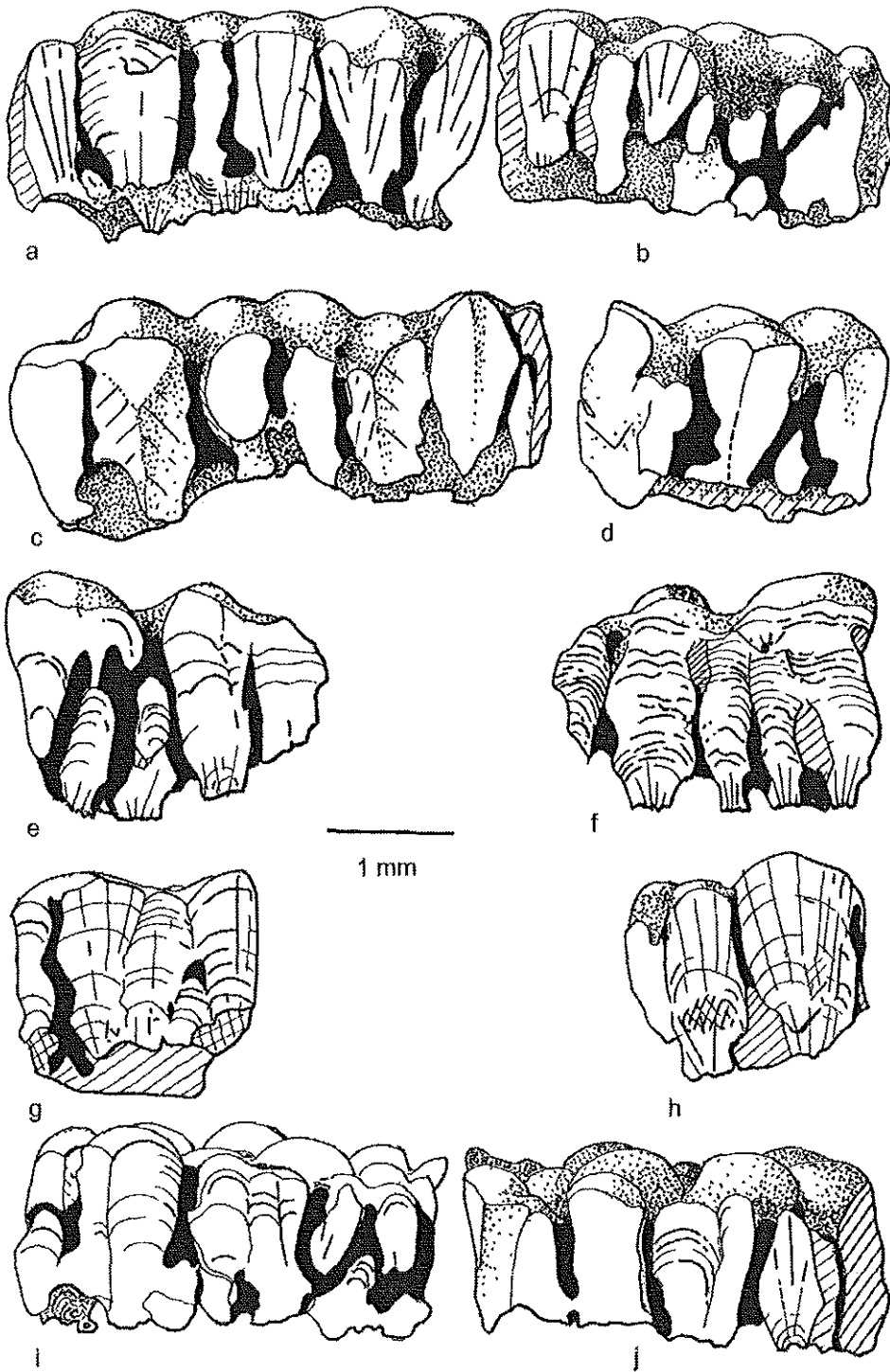


Figure 2.— Broken radial surfaces of fragments of *Megaloolithus maghrebiensis* GARCIA *et al.* (this volume), from Achlouj 2 locality, level 18-19 (Middle Atlas, Morocco), showing the organization of the units and the "reticulate" pore canal system. a,b,c,d: ACH2-370; e,f: ACH2-372; g,h: ACH2-373; i,j: ACH2-371.

*Pseudomegaloolithus atlasi* nov. oogen, nov. oospec.

(Plate 1 g to j, plate 2 d to f, figures 3-4)

In Achlouj 2 level 18-19, we have found half hundred of small fragments of the megaloolithid oospecies previously documented by only one tiny fragment from Achlouj 1 A (ACH1-3) (Garcia *et al.*, this volume). We have suggested (this Symposium) to erect a new oogenus for this oospecies, due to its peculiar features, detailed below, that separate it from typical *Megaloolithus*, like *mamillare*, *siruguei*, *microtuberculata*, *cylindricus* or *jabalpurensis* for example. We have formerly erected the oogenus *Cairanolithus* (Vianey-Liaud *et al.*, 1994) on such kind of reasons. However, two difficulties arise with this proposal. First, even if the fragments are relatively numerous, no complete egg is known. Second, in our following discussion, we underline similarities with South American eggshells fragments (from Bagua, Peru).

As we have found clear differences with *Megaloolithus*, it is possible to propose a new oogenus. Further researches would decide if this oogenus remains valid or if it has to be synonymized.

**Diagnosis of the oogenus :**

On the outer surfaces of the fragments, small (0.3 to 0.6 mm) nodes frequently fused in arched and irregular ridges, a few being isolated; nodes and ridges separated by deep valleys where the relatively wide (70 to 100  $\mu\text{m}$ ) and irregular pore canals open; units of various thickness according to their position, nodes or flat areas in valleys.

Differs from *Cairanolithus* by its fan – shaped and short units, its well rounded nodes and high ridges. Differs from *Megaloolithus* by the frequent ridges and the wide, numerous, irregular and short pore canals.

**Diagnosis of the oospecies:**

Thin Megaloolithidae (0.63 to 1.14 mm; average 0.84 mm), with irregular fan – shaped units, some being low and fused in the wide "valleys", with more or less arched growth lines (more in well separated nodes, less in flat areas); pore canals wide (70 to 150  $\mu\text{m}$ ) prolatocanaliculate, enlarged at the base of the units, and sometimes at their openings.

**Holotype, and type locality:** ACH2-206, eggshell fragment, from Achlouj 2, in grey clays, level 18-19, (Middle Atlas, Morocco), Upper Maastrichtian.

**Other localities:** ? Pont de Januc (Hérault, France); ? Takli and Pisdura (Maharashtra, India); ? Bagua (Peru, South America).

**Measurements and statistics:**

*Pseudomegaloolithus atlasi*

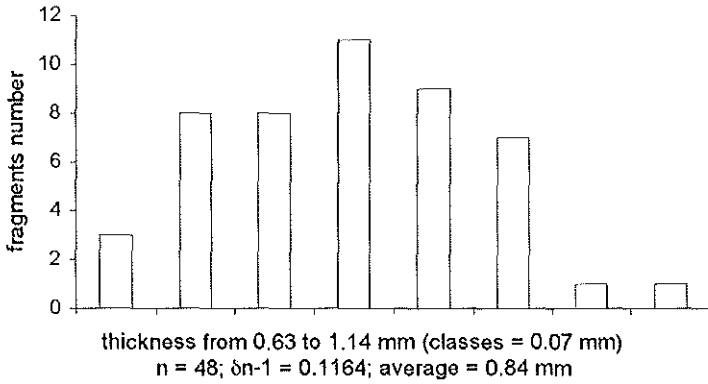


Table 2.— Measurements and statistics of *Pseudomegaloolithus atlasi* from Achlouj2.

### Description and discussion

The outer surface displays some well rounded and isolated nodes (0.3 to 0.6 mm in diameter) but they are generally arranged in chains and sinuous ridges. Nodes and ridges are separated by deep valleys, where the pores open. Pore canals are numerous and wide (0.70 to 1.50 mm), for a thin eggshell thickness varying from 0.65 to 1.14 mm (average = 0.84 mm). The pore density seems relatively important but, because of the very fragmentary material, it is not possible to calculate the conductance. The volume of the holes, going with the thinness of the eggshell explain the bad conservation. Some fragments show that the calcite bridges linking the units is sometimes less than 1/3 of the eggshell thickness! (Figures 3-4).

The irregularity of nodes and ridges, the deep valleys and the wide and irregular pore canals lead us to separate this form of the genus *Megaloolithus*. This structure resemble that formerly described from Takli and Pisdura (India), Pont de Januc, (France) and Bagua basin (Peru). In all these localities, the oospecies is only documented by a few fragments. Formerly, on the basis of microstructural similarities, Peruvian and Indian fragments have been placed in the same ootaxon *M. pseudomamillare*, defined from Les Bréguières (France). Recently, comparing Indian and French ootaxa (Vianey-Liaud *et al.*, 2003), we have suggested that *M. pseudomamillare* could be synonymized with the Indian oospecies *M. baghensis* described from Bagh Caves. But we have noted that complete eggs of these two ootaxa show differences in size of eggs and eggshell thickness. The isolated material from Morocco is significantly thinner than typical *M. baghensis* or *M. pseudomamillare*. Moreover, the numerous and irregular pore canals, generally opening in deep valleys, the irregular ornamentation of the outer surface, are not found in these Megaloolithid oospecies. But the Moroccan material closely looks like the late Maastrichtian eggshells from Bagua basin in Peru (Vianey-Liaud *et al.*, 1997).

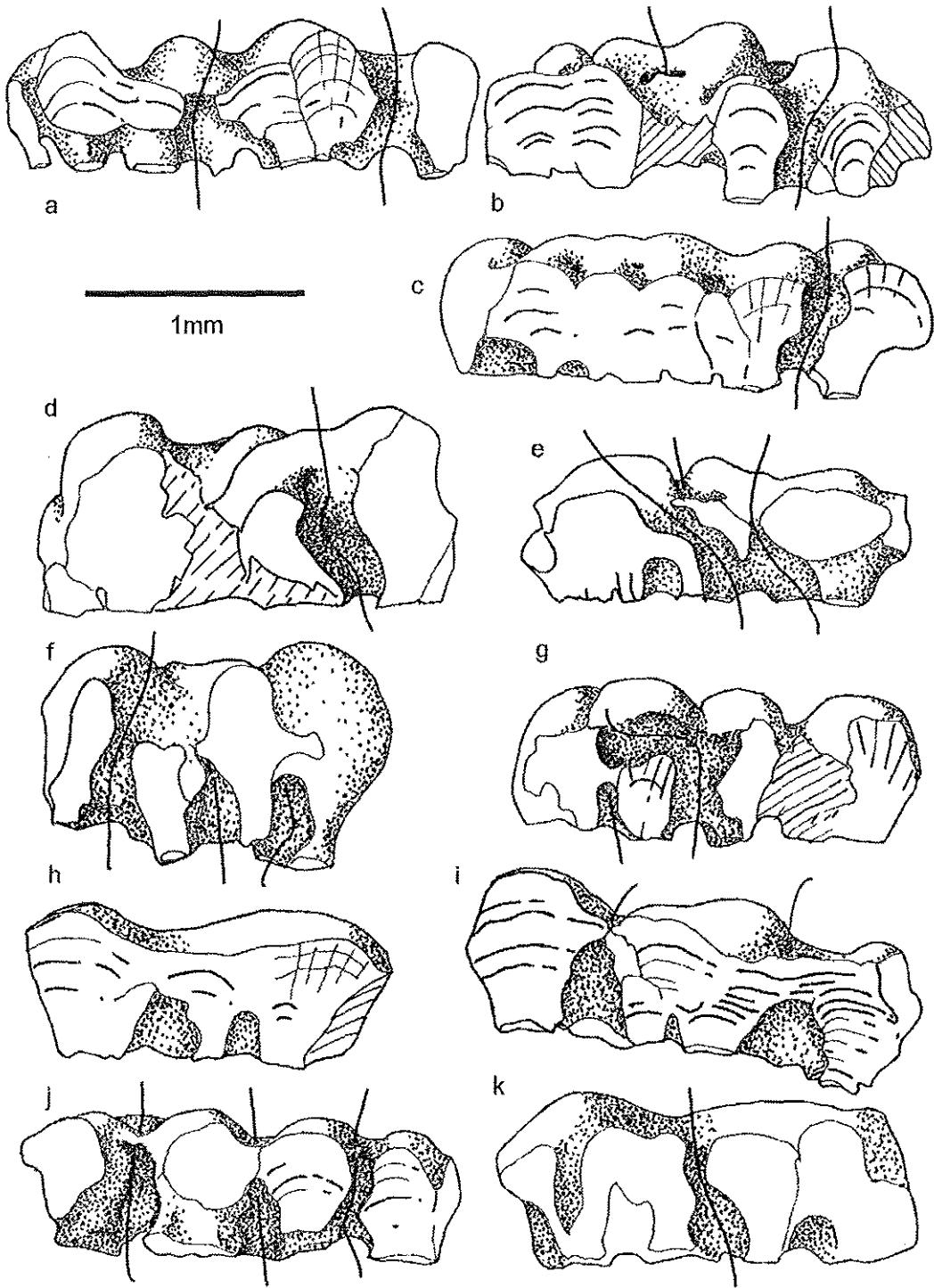


Figure 3.— Broken radial surfaces of fragments of *Pseudomegaloolithus atlasi* oogen. nov. oospec. nov., showing the organization of the units and the prolatocanalliculate pore canal system; from Achlouj 2 locality, level 18-19 (Middle Atlas, Morocco). a: ACH2-211; b: ACH2-213; c: ACH2-216; d: ACH2-220; e: ACH2-223; f: ACH2-224; g: ACH2-225; h,i: ACH2-227; j: ACH2-228; k: ACH2-237. The black lines indicate the course of the pore canals.



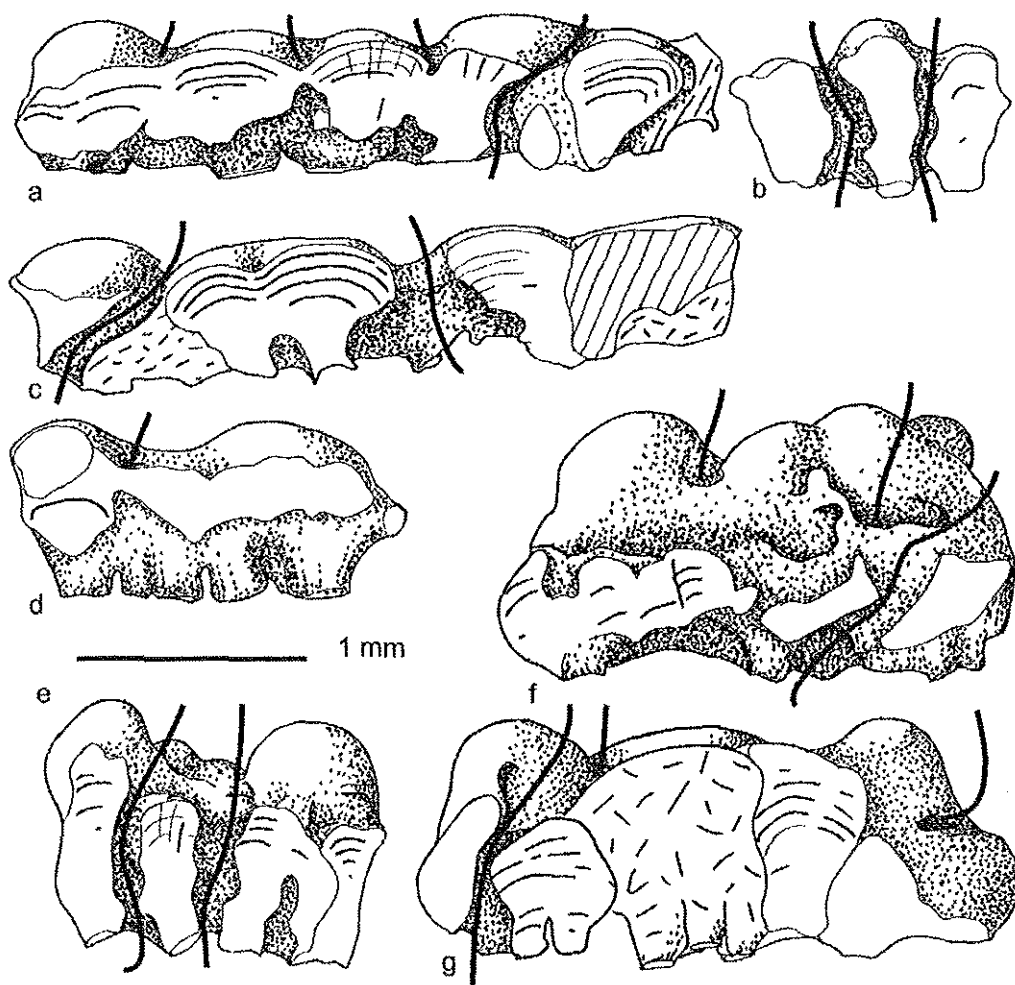


Figure 4.— Broken radial surfaces of fragments of *Pseudomegaloolithus atlasi* oogen. nov. oospec. nov., showing the organization of the units and the prolatocanaliculate pore canal system; from Achlouj 2 locality, level 18-19 (Middle Atlas, Morocco). a, c: ACH2-229; b: ACH2-243; d: ACH2-240; e: ACH2-257; f, g: ACH2-210.

Oofamily: ? ELONGATOLITHIDAE ZHAO, 1975

**Definition of the family** (from Mikhaïlov, 1991): ratite eggshell (two – layered), with the single to mammillary layer ratio ranging from 3:1 to 5:1; pore system angusticanaliculate; linearituberculate ornamentation on equatorial region tending to ramotuberculate ornamentation on the poles; elongate eggs.

*Rodolphoolithus arioul* nov. oogen. nov. oospec.

**Diagnosis** : ? elongate egg; ratite eggshell (two – layered) with rather thick mamillary layer (continuous / mamillary ratio = 3:2 to 2:1) for an Elongatoolithidae;

ramotuberculate; eggshells thin.

**Holotype:** ACH2-4, Cast of a partial egg, bearing a few eggshells fragments.

**Type locality:** Achlouj 2, levels 18 to 19, in grey clays; middle Atlas, Morocco; Upper Maastrichtian.

**Measurements and statistics:**

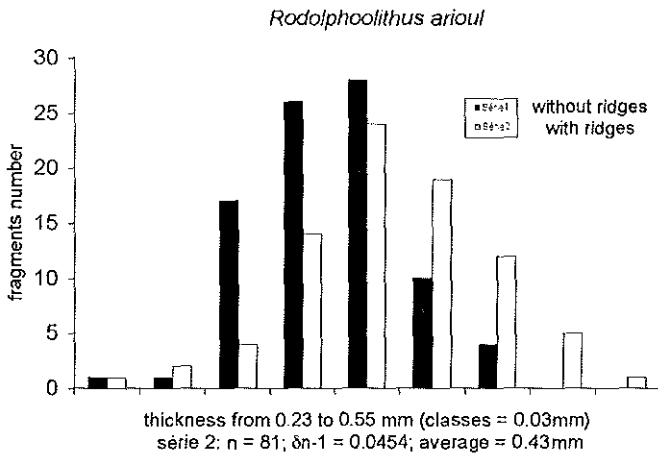


Table 3.— Measurements and statistics of *Rodolphoolithus arioul* from Achlouj2.

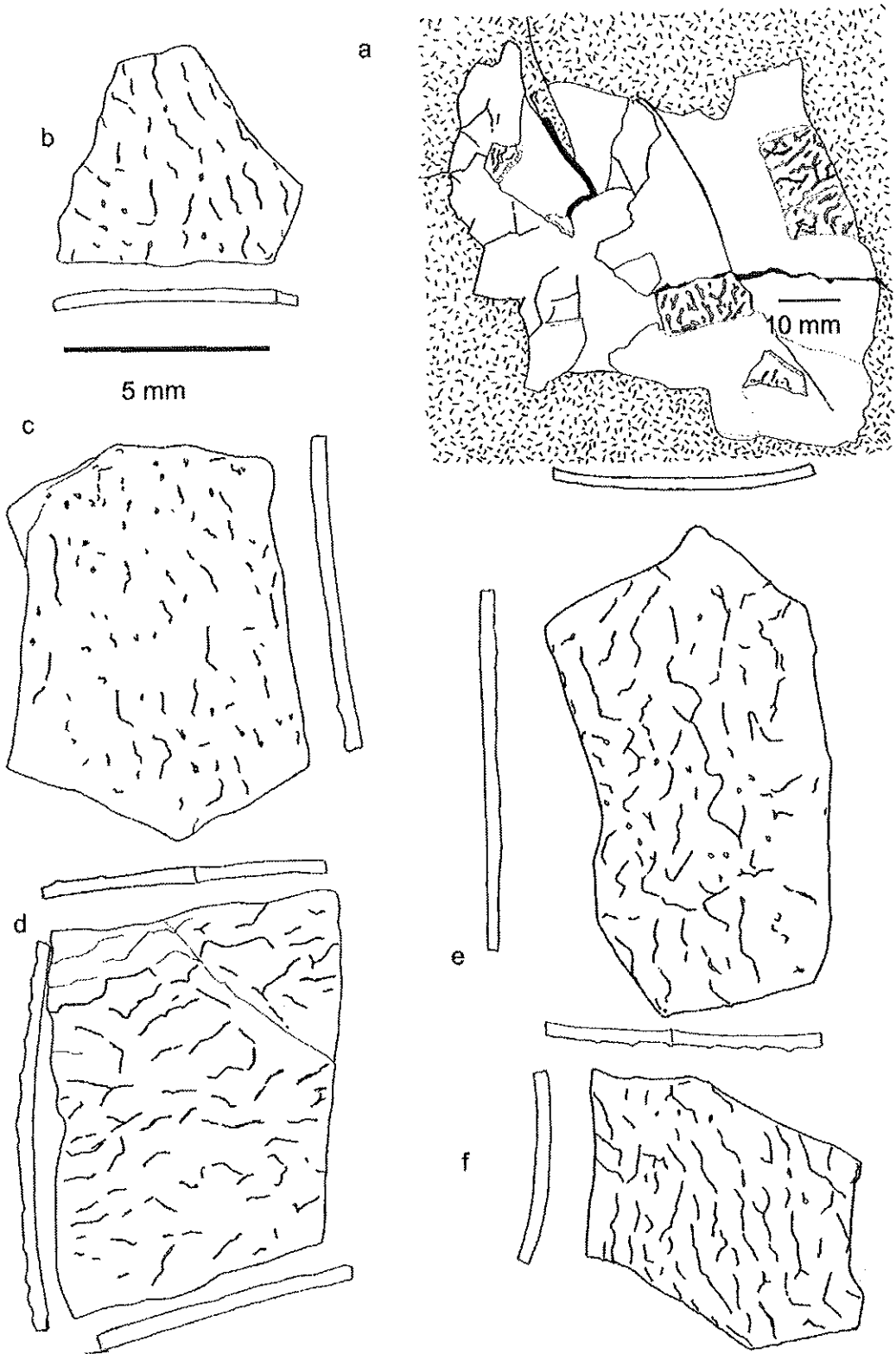
### Description and discussion

One cast of a partial egg (ACH2-4), with a few eggshells fragments preserved has been found during the excavation (Figure 5a). It was probably elongated, but the cast is not complete enough to be sure. Numerous isolated fragments (about one hundred) are flat or slightly curved, that could suit with an elongated egg (Figure 5 b to f). The outer surface is ornamented with sinuous ridges, sometimes curved, with a few isolated nodes. The ridges are low, irregular, and roughly in rows, ramotuberculate, following Mikhailov terminology. Most of the fragments are recrystallized, as shown in these SEM views (Plate 3 b-c). It seems that it is the reason why the pores are not observed on the surfaces.

Only a few thin sections are useful to detect the microstructure (ACH2-326). They clearly show two layers. The ratio between outer layer and mamillary layer is about 3 to 2, to 2 to 1. Mineralizations underline the horizontal layers of the outer layer, and the resorption craters in the mamillae cores. The eggshell are thin, and the ridges not very high. This microstructural organisation recall that of the Elongatoolithidae. The thinnest known Elongatoolithidae is *Trachoolithus*, from Mongolia (Mikhailov, 1994), but that oogenera is more linearly tuberculate, with higher sculptures, and mamillary layer more reduced (3 to1 to 4 to 1).

Figure 5.— *Rodolphoolithus arioul* oogen. nov. oospec. nov., from Achlouj 2 locality, level 18-19 (Middle Atlas, Morocco). a: ACH2-4: Natural cast of a partial egg, crushed, bearing a few fragments of eggshells.

Drawings of the outer surfaces of eggshells fragments showing the axes of the ridges and some isolated points corresponding to isolated nodes. For each fragments two views (each indicated by a black arrow) of their radial profiles are given. b: ACH2-23; c: ACH2-15; d: ACH2-7; e: ACH2-5; f: ACH2-9.



**Definition of the family** (from Mikhaïlov, 1991): single continuous layer thinner than mammillary layer and varying to 1:2 to 1:3; angusticanalicate eggshell; surface smooth to microsculptured (microtubercles); thin eggshells, from 0.3 mm to 1.05 mm (microsculptures included)

*Tipoolithus achloujensis* GARCIA *et al.*, this volume

**Diagnosis** : Subtiliolithidae with rather thick eggshell (0.43 to 0.73 mm, between the high irregular nodes, and from 0.55 to 1.04 mm including the nodes); dispersituberculate, with high nodes (ratio node height: eggshell thickness 0,37 to 0,40); pore openings situated from top of the nodes to their base, or between them; wide pore openings (90 to 160 µm); angusticanalicate pore system.

**Holotype and type locality**: ACH2-284, thin section of an eggshell fragment; Achlouj 2, levels 18 to 19, in grey clays; middle Atlas, Morocco; Upper Maastrichtian.

**Measurements and statistics**:

*Tipoolithus achloujensis*

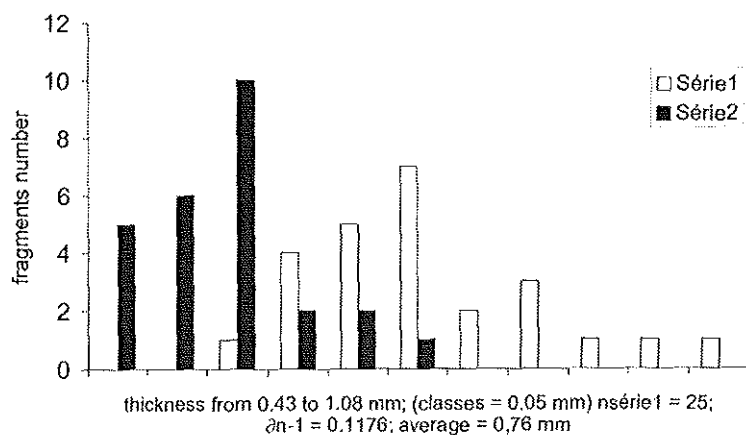


Table 4.— Measurements and statistics of *Tipoolithus achloujensis* from Achlouj2. Serie 1 = thickness including nodes; serie 2 = thickness without nodes.

## Discussion

Additional material (Plate 4) to that previously described allows to extend the eggshell thickness from 0.40 to 0.73 mm. Including the high nodes, total thickness vary from 0.55 to 1.04 mm. The oospecies is questionably referred to the Subtiliolithidae. In this oofamily, the mamillary layer is thicker than the outer layer (1:2, to 1:3). It is the case in *Subtiliolithus kahchensis*, from India (Khosla & Sahni, 1995), or *Porituberoolithus warnerensis* from north America (Zelenitsky *et al.*, 1996), where the nodes are clearly lower than in our north African eggshells. Moreover, even if the mamillary layer is here thicker than the outer layer, it is less (1:1,5) than in the Indian and American Subtiliolithidae.

Oofamily: PRISMAToolithidae HIRSCH, 1994, emend. Zelenitsky & Hills, 1996

Definition of the family : cf. Zelenitsky & Hills, 1996

Oogenus *PEUDOGECKoolithus* VIANEY-LIAUD & LOPEZ-MARTINEZ, 1997

**Definition:** eggshell with prismatic two-layered structure; short mamillary layer (1/10 to 1/8); outer surface with rare and irregular nodes; wide pores canals situated at the top of the nodes.

? *Pseudogeckoolithus tirboulensis*, oospec. nov.

= ? *Prismatoolithus* indet. in GARCIA *et al.*, this volume

**Diagnosis:** thin prismatic eggshell (0,22 to 0,36 mm including nodes, and 0,13 to 0,29 mm between nodes); dispersituberculate with nodes diameters varying from 0,05 mm to 0,25 mm; inner layer generally as thick as the outer layer.

**Holotype and type locality:** ACH2-330, thin section of an eggshell fragment; Achlouj 2, levels 17 to 19, in grey clays; middle Atlas, Morocco; Upper Maastrichtian.

**Measurements and statistics:**

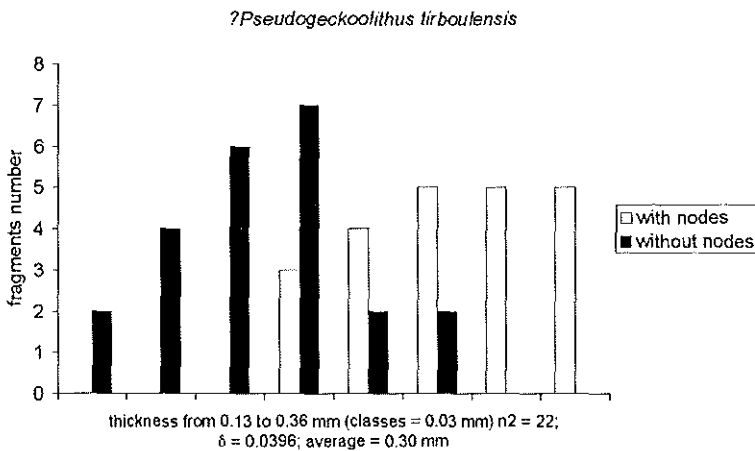


Table 5.— Measurements and statistics of ? *Pseudogeckoolithus tirboulensis* from Achlouj2.

## Description

We tentatively include this oospecies within the oogenus *Pseudogeckoolithus*, because of the prismatic structure, of the node pattern and of the location of pore openings at the top of some nodes. But the inner layer is much thicker than in the type oospecies *P. nodosus* from Spain (1/2 to 1/3 compare to 1/8 to 1/10).

25 fragments of very thin eggshells from Achlouj 2 allow to describe another oospecies. It is dispersituberculate, and nodes are 0.05 to 0.25 mm in diameter. The total eggshell thickness vary from 0.22 to 0.36 (0.13 to 0.29 without ornamentation). As prisms are visible in thin sections, continue from the inner layer to the outer layer, we include it in the Prismaticolothidae (Plate 6). SEM observations show wedges with tabular crystal in the mamillary layer, whereas it is clearly distinct of a spongy outer layer (Plate 5). The mamillary layer is nearly as thick as the spongy one or slightly thinner.

Pore are hardly distinguishable on the surfaces due to calcite recrystallisations and quartz embedments. Some seem to be placed at the top of a few nodes (Figure 6). But we have not yet seen them in thin sections. As far as the location of pores could be confirmed, the thickness, ornamentation, and microstructure recall that of *Pseudogeckoolithus*, described from Southern France and Northern Spain (Vianey-Liaud & Lopez-Martinez, 1997; Garcia *et al.*, this volume).

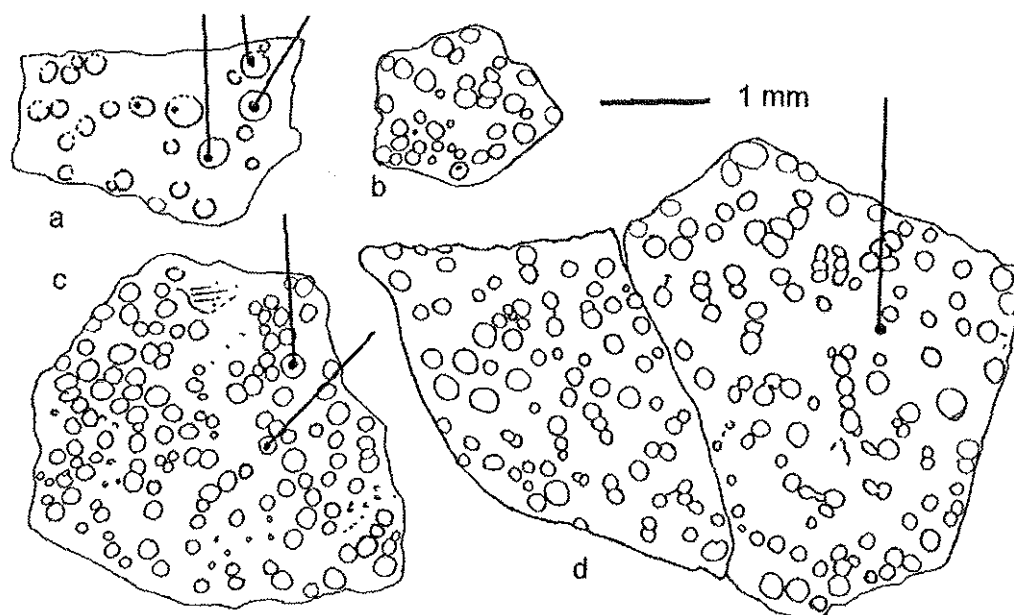


Figure 6.— Outer surface of fragments of ? *Pseudogeckoolithus tirboulensis* oospec. nov., from Achlouj 2 locality, level 18-19 (Middle Atlas, Morocco) showing the dispersed nodes. A few pores seem to be located at the top of nodes (indicated by black lines); only one, on d, open in a flat area. a: ACH2-337; b: ACH2-355; c: ACH2-338; d: ACH2-341.

## DISCUSSION AND CONCLUSION

Until our discovery, the record of Maastrichtian African dinosaur was empty. Even if we have not recorded entire skeletons, a few teeth remains (Garcia *et al.*, this volume) and these eggshells fragments recorded in sediments of the Oukdiksou

syncline, Middle Atlas from Morocco, give some light on the Late Cretaceous dinosaur African fauna. Even if fragmentary, the diversity of the eggshells indicates that the fauna comprises at least five dinosaur oospecies.

Among them, the vegetarians are documented by the Megaloolithidae, that indicates the probable occurrence of at least one titanosaurid Sauropod, even if we are not sure that the whole oogenera and oospecies of the oofamily Megaloolithidae correspond only to the titanosaurids (Vianey-Liaud *et al.*, 2003). This discovery fills the African gap in the gondwanian distribution of the Megaloolithidae oofamily, that bears evidence for Gondwanian Maastrichtian exchanges, and reasserts the communication between Southern Europe and Gondwana.

Some Elongatoolithidae (Norell *et al.*, 1994, 1995; Dong & Currie, 1996) and Prismatoolithidae (Hirsch & Quinn, 1990; Zelenitsky & Hills, 1996; Varrichio *et al.*, 1999; Makovicky & Grellet-Tinner, 2000) have been referred to non avian theropods, due to discoveries of embryos inside eggs. The occurrence of *Rodolphoolithus* and *Pseudogeckoolithus* could show that at least two species of probably small carnivore theropods were present in North Africa. If we follow Mikhailov (1991, p. 222), *Tipoolithus*, questionably referred to the ? Subtiliolithidae, could correspond either to non avian or avian theropods, of a greater size.

#### ACKNOWLEDGEMENTS

This work has got financial support from UMR-UM2-CNRS-5554; ISEM and by the ECLIPSE-CNRS program.

Many thanks to the Moroccan field team, especially Rodolphe Tabuce, Bernard Marandat, Henri Cappetta, Ilhem Bentaleb and Aziza BenAbdallah.

#### REFERENCES

- DONG, Z.-M. & CURRIE, P.J., 1996. — On the discovery of an oviraptorid skeleton on a nest of eggs at Bayan Mandahu, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences*, 33: 631-636.
- GARCIA, G., 2000. — Diversité des coquilles « minces » d'œufs fossiles du Crétacé supérieur du Sud de la France. *Géobios*, 33 (1) : 113-126.
- GARCIA, G. & VIANEY-LIAUD, M., 2001. — Nouvelles données sur les coquilles d'œufs de dinosaures Megaloolithidae du Sud de la France : systématique et variabilité intraspécifique. *Comptes Rendus de l'Académie des Sciences*, Paris, Sciences de la Terre et des Planètes, 332 : 185-191.
- GARCIA, G., FEIST, M., CABOT, A., VALENTIN, X. & VIANEY-LIAUD, M., 2000. — Les œufs de dinosaures du Crétacé supérieur du bassin de Villeveyrac – Mèze (Hérault, France) : description d'une nouvelle espèce de *Prismatoolithus*, *Bulletin de la Société Géologique de France*, 171 (3) : 282-289.
- GARCIA, G., TABUCE, R., CAPPETTA, A., MARANDAT, B., BENTALEB, I., BEN ABDALLAH, A.

- & VIANEY-LIAUD, M., 2003. — First dinosaur eggshells and bone discovery in North African Maastrichtian (Morocco), *Palaeovertebrata*, 32 (2-4): 59–69, 1 fig., 1 pl.
- HIRSCH, K., 1994. — The fossil record of vertebrate eggs : 269-294, In Donovan, S.K. (ed.) : The Paleobiology of Trace Fossils. *John Wiley & Sons*, London.
- HIRSCH, K. & QUINN, B., 1990. — Eggs and eggshell fragments from the upper Cretaceous Two Medicine formation of Montana. *Journal of Vertebrate Paleontology* 10: 491-511.
- KHOSLA, A. & SAHNI, A., 1995. — Parataxonomic classification of Late Cretaceous dinosaur eggshells from India, 40 : 87-102.
- MAKOVICKY, P.J. & GRELLET-TINNER, G., 2000. — Association between theropode eggshell and a specimen of *Deinonychus antirrhopus*. In "First International Symposium on Dinosaur Eggs and Babies", Isona, Spain, Extended Abstracts: 123-128.
- MIKHAĬLOV, K.E., 1991. — Classification of fossil eggshells of amniotic vertebrates. *Acta Paleontologica Polonica*, 36: 193-238.
- MIKHAĬLOV, K.E., 1994. — Theropod and Protoceratopsian Dinosaur Eggs from the Cretaceous of Mongolia and Kazakhstan. *Paleontological Journal*, 28(2): 101-120.
- MIKHAĬLOV, K.E., 1997. — Fossil and recent eggshell in amniotic vertebrates: fine structure, comparative morphology and classification. *Special Papers in Paleontology*, 56: 1-80.
- MIKHAĬLOV, K.E., BRAY, E. & HIRSCH, K., 1996. — Parataxonomy of fossil egg remains (Veterovata) : principles and applications. *Journal of Vertebrate Paleontology*, 16(4) : 763-769.
- NORELL, M.A., CLARK, J.M., DASHEVEG, D., RHINCHEN, B., CHIAPPE, L.M., DAVIDSON, A.R., MCKENNA, M.C., ALTAZNGEREL, P. & NOVACEK, M.J., 1994. — A theropod dinosaur embryo and the affinities of the Flaming Cliffs dinosaur eggs. *Science*, 266 :779-782.
- VARRICCHIO, D.J., JACKSON, F. & TRUEMAN, C.N., 1999. — A nesting trace with eggs for the cretaceous theropod dinosaur *Troodon formosus*. *Journal of Vertebrate Paleontology*. 19(1): 91-100.
- VIANEY-LIAUD, M. & LOPEZ-MARTINEZ, N., 1997. — Late Cretaceous dinosaur eggshells from the Tremp basin (Southern Pyrenees, Lleida, Spain). *Journal of Paleontology*, 71: 1157-1171.
- VIANEY-LIAUD, M & GARCIA, G., 2000. — The interest of French Late Cretaceous dinosaur eggs and eggshells. In "First International Symposium on Dinosaur Eggs and Babies", Isona, Spain, Extended Abstracts: 165-176.
- VIANEY-LIAUD, M., KHOSLA, A. & GARCIA, G., 2003. — Comparisons of European and Indian dinosaurs eggshells ; paleobiogeographical implications. *Journal of vertebrate Paleontology*, 23(3) : 575-585.
- ZELÉNITSKY, D.K. & HILLS, L.V., 1996. — An egg clutch of *Prismatoolithus levis* oosp. Nov. from the Oldman Formation (Judith River Group; Upper Cretaceous), southern Alberta. *Canadian Journal of Earth Sciences*, 33: 1127-1131.
- ZELÉNITSKY, D.K. ,HILLS, L.V. CURRIE, P.J., 1996. — Parataxonomic classification of ornithoid eggshell fragments from the Oldman Formation (Judith River Group; Upper Cretaceous), southern Alberta. *Canadian Journal of Earth Sciences*, 33: 1655-1667.



## CAPTIONS OF THE PLATES

### PLATE 1

*Megaloolithus maghrebiensis* GARCIA *et al.* (this volume), from Achlouj 2 locality, level 18-19 (Middle Atlas, Morocco). a: ACH2-197, SEM view of the outer surface of an eggshell fragment; b, c, d: ACH2-200, SEM radial view; e, f: ACH2-201, SEM radial view.

*Pseudomegaloolithus atlasi* oogen. nov. oospec. nov., from Achlouj 2 locality, level 18-19 (Middle Atlas, Morocco). g: ACH2-206, SEM view of the outer surface of an eggshell fragment; h: ACH2-205 (Holotype), SEM view of the outer surface of an eggshell fragment; ei, j: ACH2-209, SEM radial view.

### PLATE 2

*Megaloolithus maghrebiensis* GARCIA *et al.* (this volume), from Achlouj 2 locality, level 18-19 (Middle Atlas, Morocco). Detail os of the Holotype thin section ACH2-1a, showing the growth lines, the junctions of the units and some features of the pore system. a: showing tangential connections of the pore canals; b: showing an "intra" spherulite; c: showing a radial course of a pore canal.

*Pseudomegaloolithus atlasi* oogen. nov. oospec. nov., from Achlouj 1 locality and Achlouj 2 locality, level 18-19 (Middle Atlas, Morocco). Thin sections of three eggshells fragments, showing the great variability of the fan shaped units heights. The black lines show the openings of wide and deep pore canals. d: ACH2-281; e: ACH2-282; f: ACH1-3.

### PLATE 3

*Rodolphoolithus arioul* oogen. nov. oospec. nov., from Achlouj 2 locality, level 18-19 (Middle Atlas, Morocco). SEM views (a, b, c, g) and thin sections (d, e, f). a: ACH2-202, outer surface, showing the irregular ridges; b, c: ACH2-204, enlarged radial view: the strong recrystallization has hidden the layering; d: ACH2-326, enlarged thin section showing the separated mammillae, and their core underlined by an arched mineralization; e, f: ACH2-326, polarized (e) and natural light (f) thin section displaying the two eggshell layers (mamillary and outer); g: ACH2-204, radial view of a fragment showing the light curve of the eggshell, and the weak height of the ridges.

### PLATE 4

*Tipoolithus achloujensis* GARCIA *et al.* (this volume), from Achlouj 2 locality, level 18-19 (Middle Atlas, Morocco). a: ACH2-300 and b: ACH2-299, SEM views of outer surfaces of fragments, showing a dispersituberculate pattern; c: ACH2-301, SEM radial

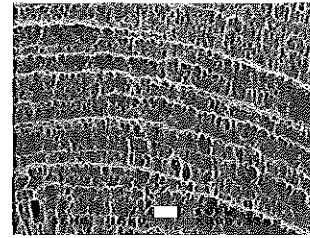
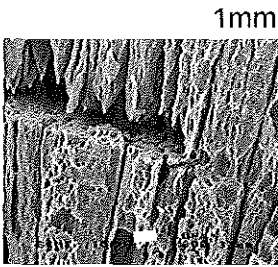
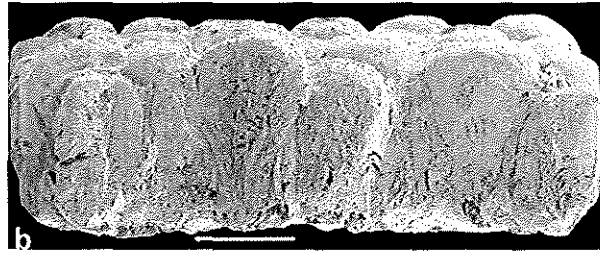
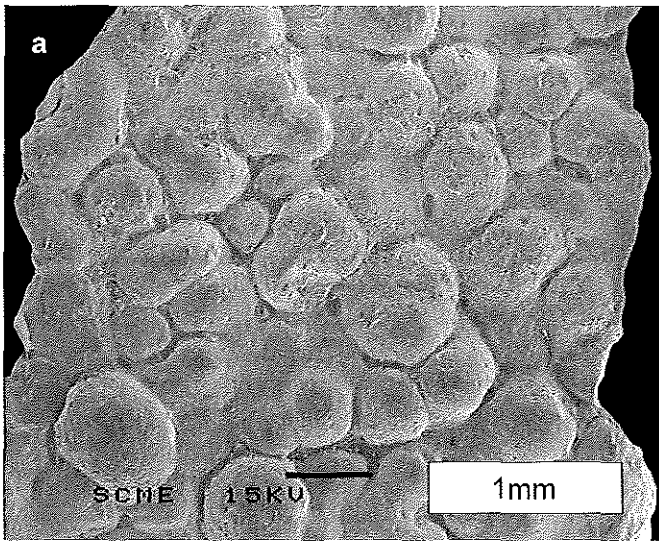
view of a fragment, showing the very high node; d: ACH2-96, thin section showing the mamillary layer thicker than the outer layer; e: id., enlarged, shows that the mamillae are as wide as high; f: ACH2-284, Holotype.

#### PLATE 5

? *Pseudogeckoolithus tirboulensis* oospec. nov., from Achlouj 2 locality, level 18-19 (Middle Atlas, Morocco). a: ACH2-331, SEM view, outer surface; b: ACH2-332, SEM view, outer surface; c,d: ACH2-333, SEM radial view, the microstructure is preserved, even if there are some voids (v) between a few growth planes; e: ACH2-334, SEM radial view, the fragment is completely recrystallized, and the microstructure is not preserved; f, g: ACH2-333, enlarged SEM radial view, f = outer (spongioid) layer, g = mamillary layer showing the wedges and tabular crystals.

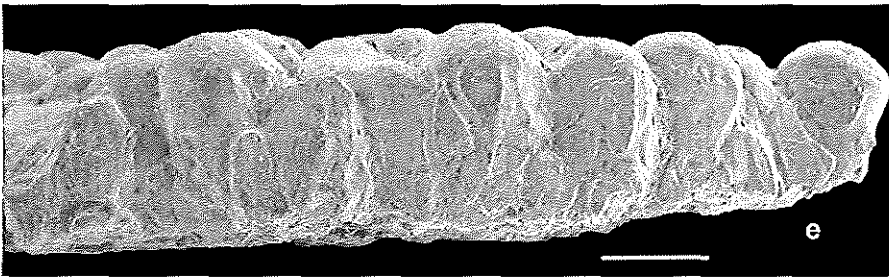
#### PLATE 6

? *Pseudogeckoolithus tirboulensis* oospec. nov., from Achlouj 2 locality, level 18-19 (Middle Atlas, Morocco). Thin sections showing the inner layer as thick as the outer layer, the low nodes, the prisms, continuous from the base to the top of the units. a: ACH2-327; b: ACH2-329, Holotype; c: ACH2-330.

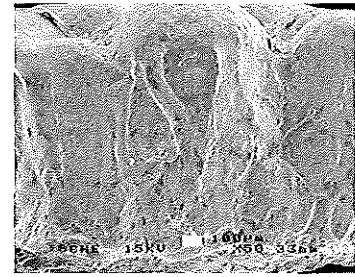


c 10µm

d 10µm

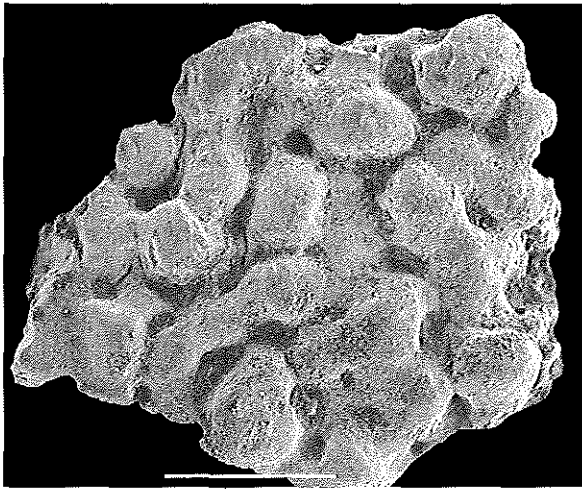


e 1mm



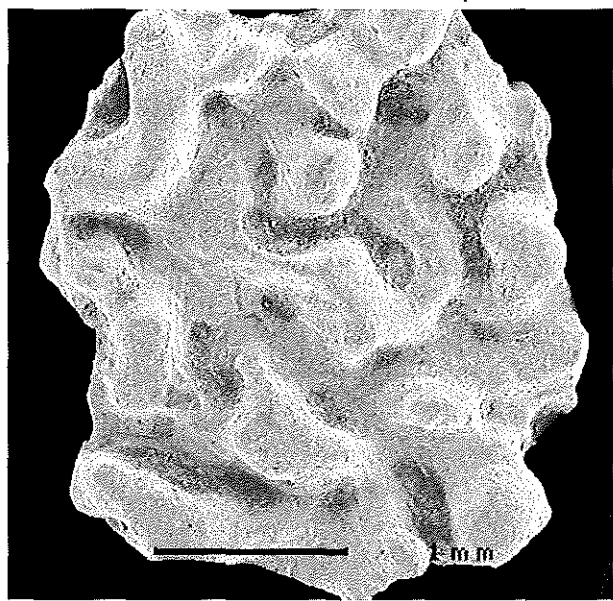
f

100µm

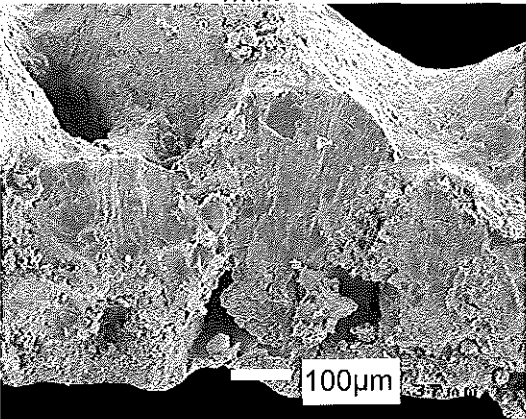


g h

1mm

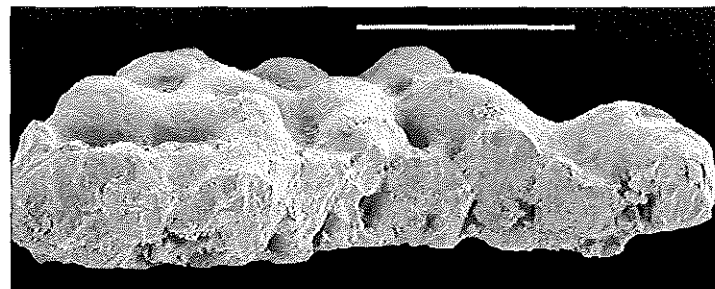


1mm

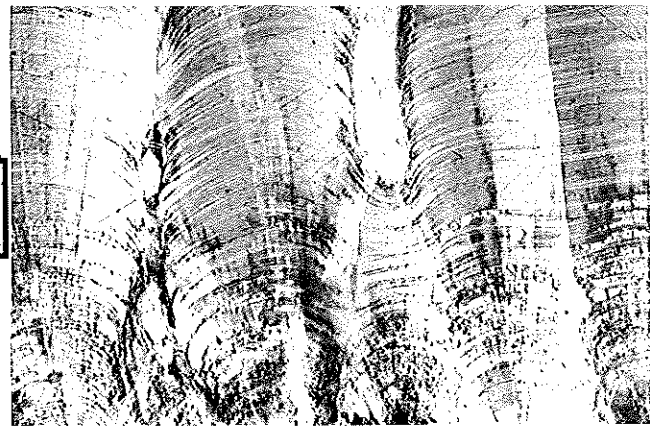
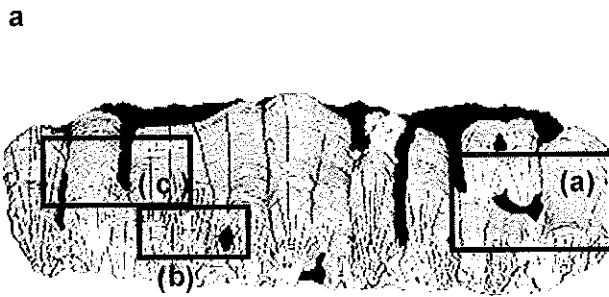


i

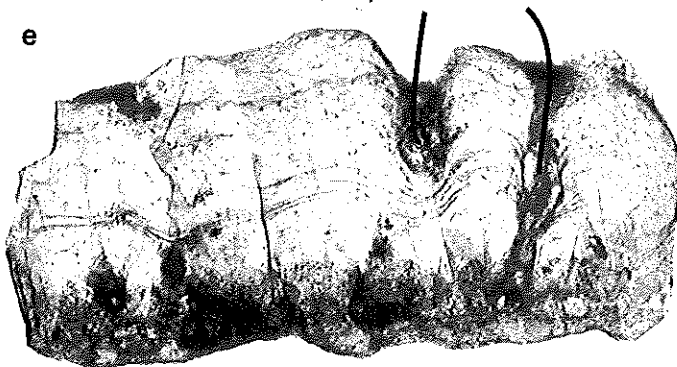
100µm



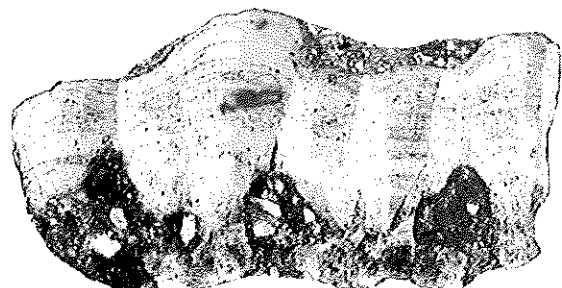
j

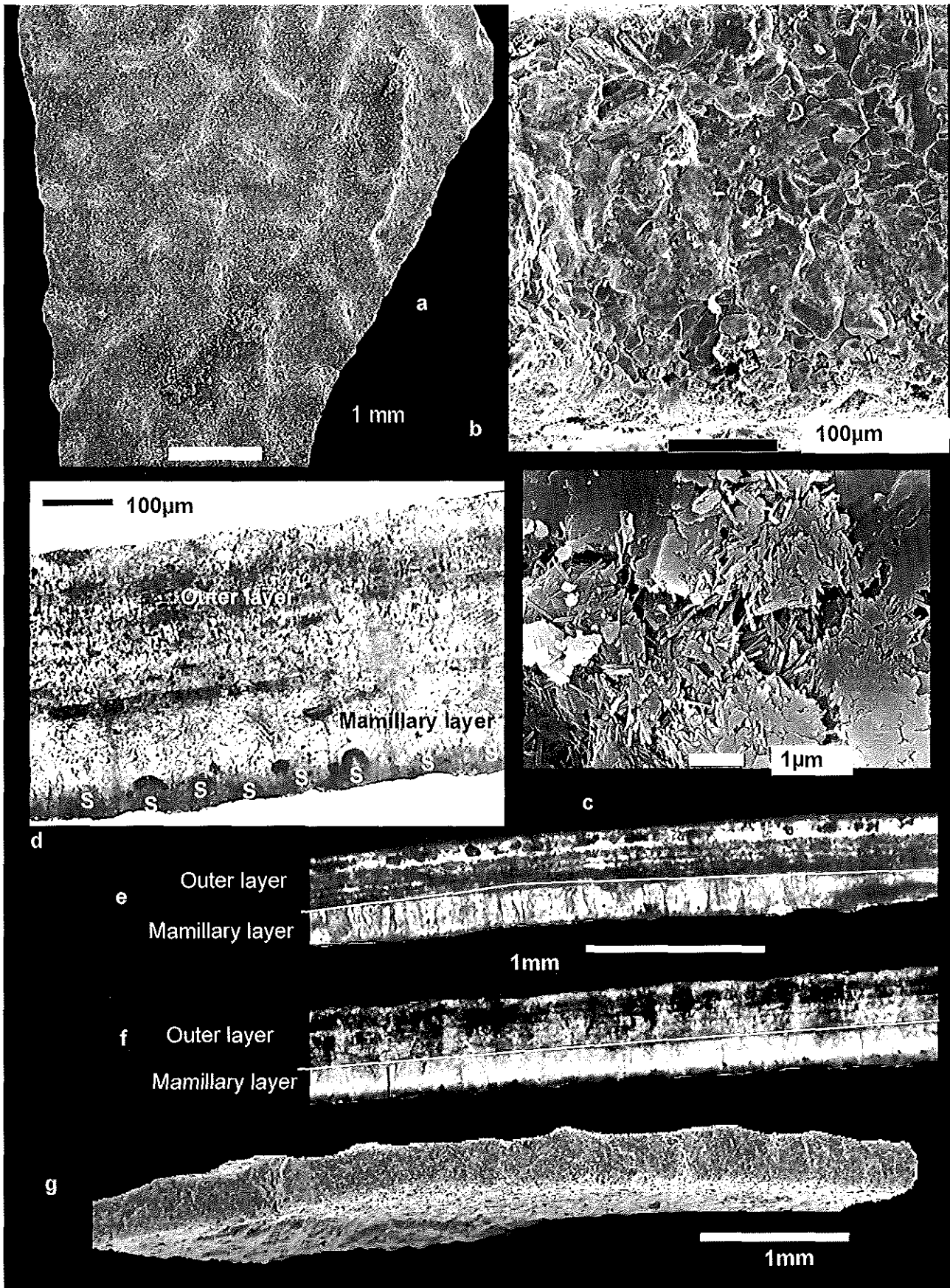


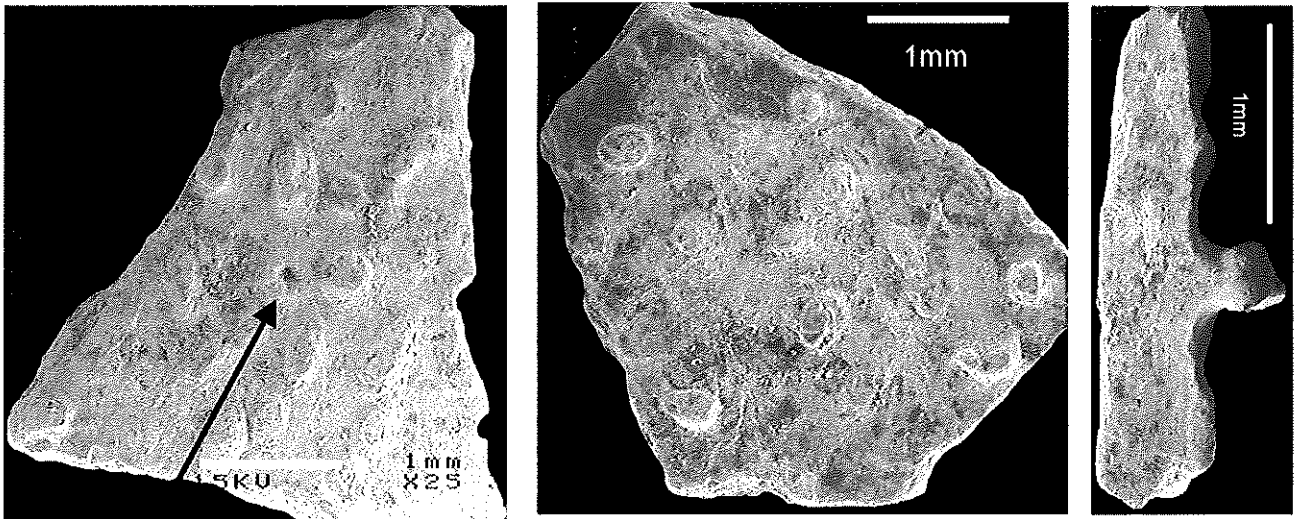
1 mm



f







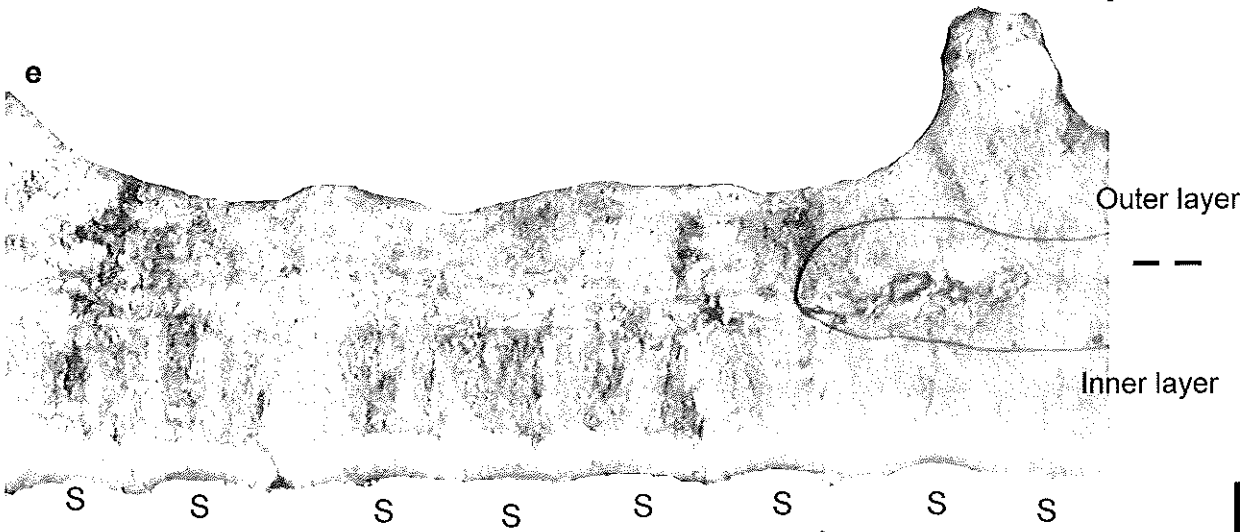
a pore opening

b

c

d

1 mm



Outer layer

Inner layer

Pore canal

f

1 mm

