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Article

First chelonian eggs and carapace fragments from the Pliocene of Rhodes, Greece

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With 8 figures and 2 tables

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Abstract: Well-preserved fossil eggs and eggshell fragments from the Pliocene Apolakkia Formation of Rhodes (Greece) are described. The eggs were found in-situ in a clutch. They are sub-spherical with lengths of 53-60 mm and widths of about 40 mm. All eggs are diagenetically compressed and their original diameters are estimated at 45-50 mm. The eggshells are 0.3-0.5 mm thick, partly recrystallized, but widely still aragonitic. They consist of needle-like crystals that form individual shell units. A few pores are preserved between these shell units. This shell-structure allows assignment to chelonian eggs in the oofamily Testudoolithidae and the oogenus *Testudolithus*. The external morphology, microstructure and mineralogical composition of the eggshells show close resemblance to eggs of the extant tortoise *Geochelone elephantopus*. Together with a small association of turtle carapace fragments from the same formation, the clutch represents the first discovery of turtle and reptilian remains from the Pliocene of the island of Rhodes.

Key words: Testudinata, eggs, clutch, Rhodes, Pliocene, Apolakkia Formation.

1. Introduction

The Pliocene Apolakkia Formation is exposed near the town of Apolakkia in the south-western part of the Greek island of Rhodes (Fig. 1). The formation contains a diverse mammalian fauna comprising five taxa of insectivores (*Crocidura* sp., Blairinini gen. et sp. indet., *Barinella* sp., *Episoriculus gibberodon*, Echinosoricinae gen. et sp. indet.), one lagomorph (*Ochotonoides* sp.) and four species of rodents (*Castor fiber*, *Mimomys occitanus*, *Dolomys* sp., and *Apodemus* aff. *dominans*) (VAN DE WEERD et al. 1982). Ungulates include *Hipparion* aff. *crassum*, *Cervus* aff. *philisi* and *Gazella* sp. and indeterminate species of Rhinocerotidae and Proboscidea (VAN DE WEERD et al. 1982). Large carnivores are represented by *Hyaena pyrenaica*, undetermined canids (VAN DE WEERD et al. 1982), and a large fragment of a canine tooth from a sabertooth cat (RICHTER 1997). Additionally, THEODOROU et al. (2000) described the elephant *Anancus arvenensis* from a Lower Pleistocene locality in Apolakkia. Invertebrates are mainly represented by the freshwater gastropods *Theodoxus hellenicus*, *Melanopsis orientalis* and *Melanoides tuberculata* (WILLMANN 1981).

The faunal composition of the Apolakkia Formation suggests that it was formed during the Middle and Late Ruscinian, i.e., about 5.3-3.4 Ma (VAN DE WEERD

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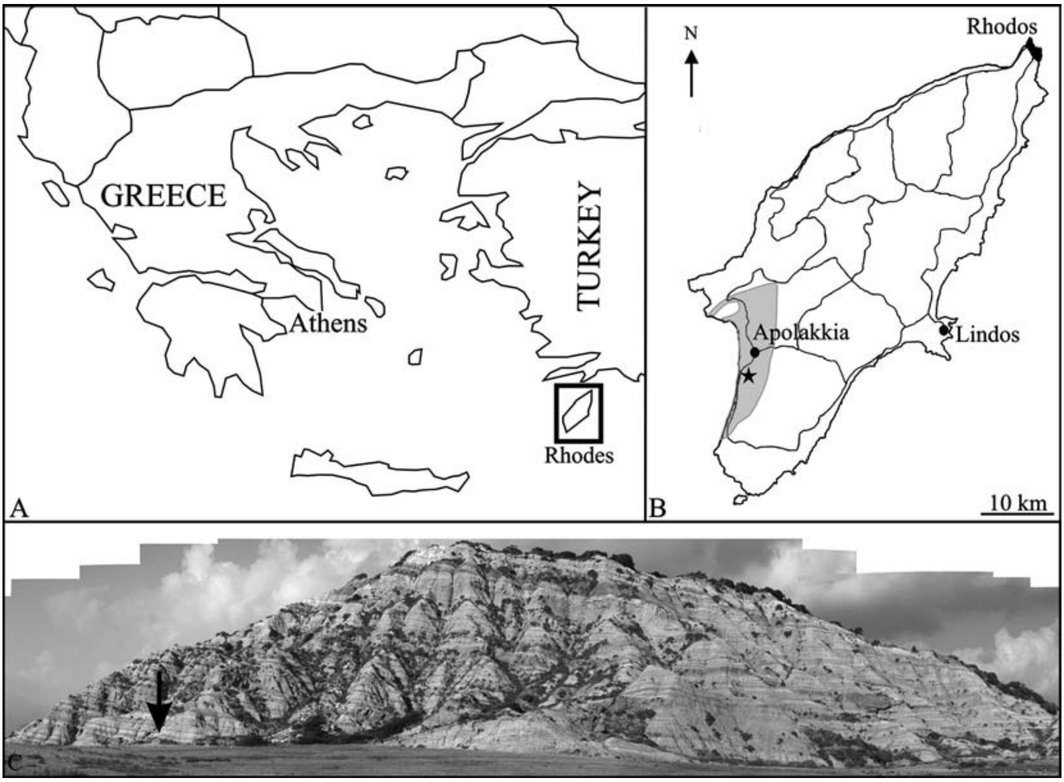
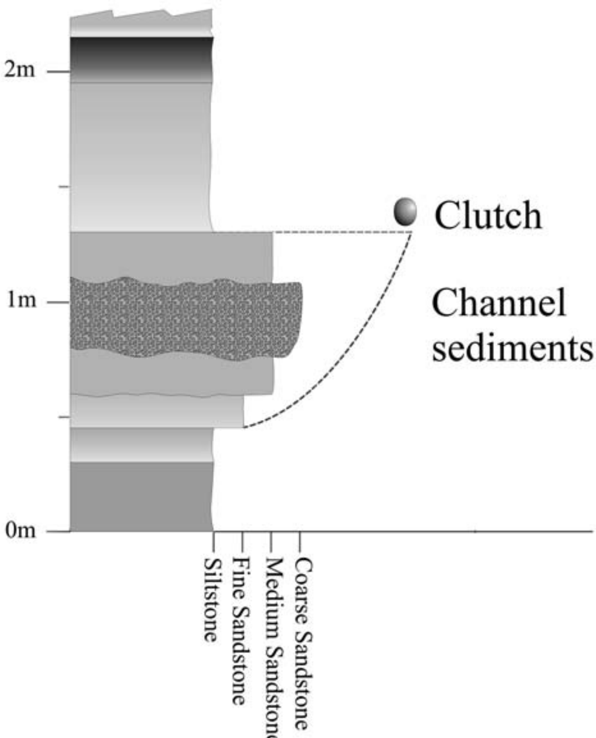


Fig. 1. A – The Greek island of Rhodes is situated just south of mainland Turkey in the Mediterranean Sea. **B** – The Apolakkia Formation (indicated by shaded area) is located in the south-western part of Rhodes and most prominently exposed just south of the town Apolakkia. The star indicates the studied locality. **C** – Photo mosaic of the Apolakkia Formation taken from the road just west of the main exposure. Arrow indicates the egg locality.



et al. 1982; Benda et al. 1987), an age determination that was recently corroborated by a palaeomagnetic study (van Hinsbergen et al. 2007).

Our study describes five spherical eggs and a number of eggshell fragments excavated from an in-situ fossil egg clutch discovered in the spring of 2005. The egg clutch together with a small association of turtle carapace fragments, found in the autumn of 2007 represent the first records of fossil reptile remains from the Pliocene of Rhodes.

Fig. 2. Sketch of the section of the Apolakkia Formation where the clutch was found just above a channel sequence. The colours in the figure are not identical with the original colours of the sediment, but they indicate colour changes within single beds or colour changes between beds.

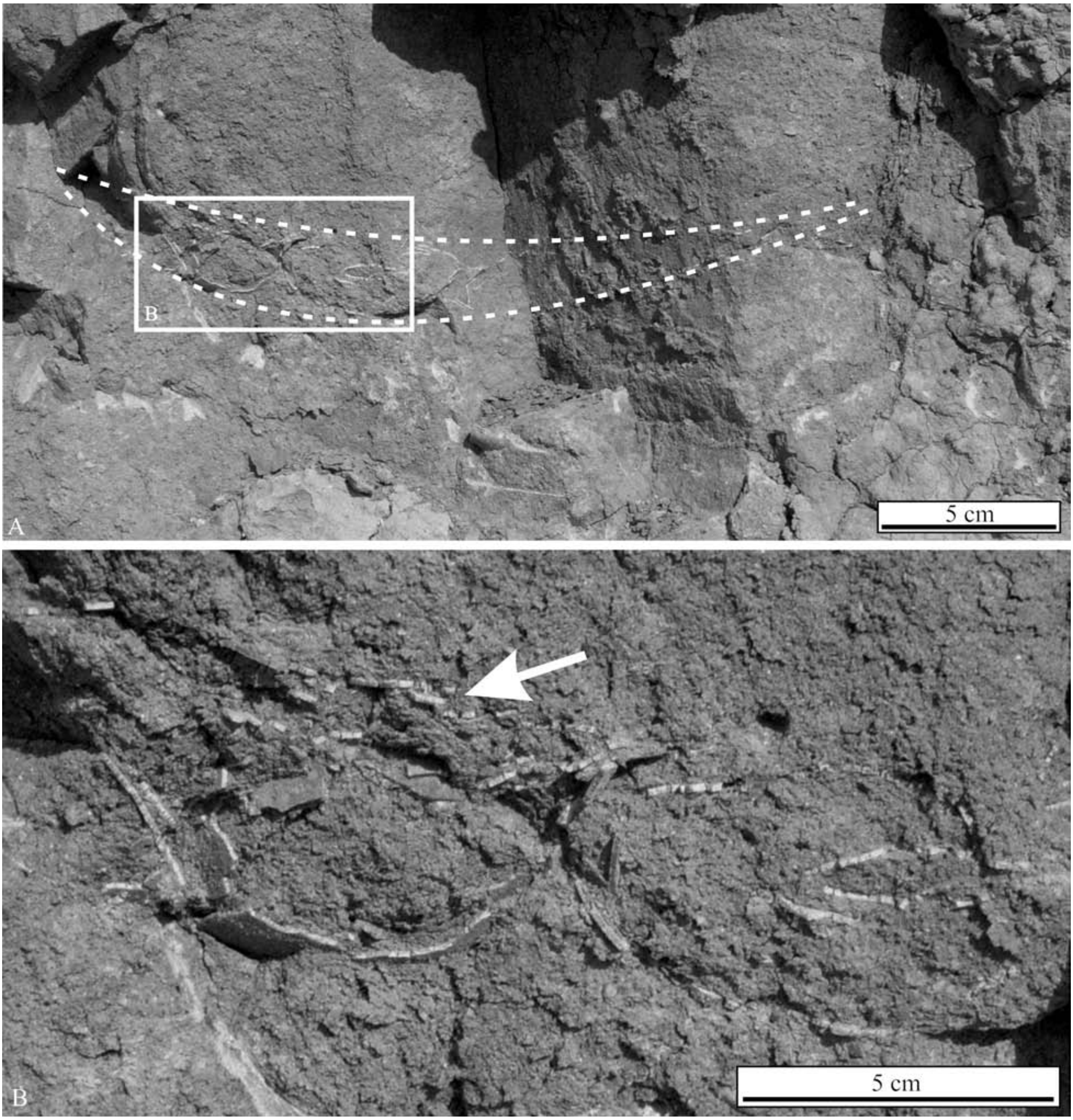


Fig. 3. A – The clutch of eggs (in-situ), exposed in cross section. The clutch forms a shallow bowl-shaped structure approximately 30 cm wide. Inserted box is enlarged section shown in B. **B** – Close-up photo showing two relatively uncrushed eggs lying side by side in the semi-consolidated sediment. Directly above the eggs there is a layer of crushed eggshell fragments (arrow).

2. Geological setting

During the Pliocene, the Island of Rhodes was part of a large fluvio-lacustrine sedimentary basin. The Apolakkia sub-basin was undergoing continuous subsidence, which facilitated deposition of about 700 m of terrestrial sediments (Duranti 1997). Its sediment supply largely arrived from the N-NE (Mutti et al. 1970; Meulenkamp et al. 1972; van Vugt & Langereis 2000). The Apolakkia Formation overlies

Table 1. Measurements of the investigated egg specimens.

Specimen	egg-shell thickness mm	egg length mm	egg width mm	egg height mm	Estimated egg diameter mm
AMPG 515	0.5	56	53	38	55
AMPG 516	0.35	54.5	51.7	44	53
AMPG 517	0.4	62	58		60
AMPG 518	0.25	54	52		53
AMPG 519	0.3-0.5				~ 50
Fragments	0.3-0.5				

the Istrios Formation (Meulenkamp et al. 1972) and its top grades into the Monolithos Formation, which consists of freshwater limestones (Mutti et al. 1970).

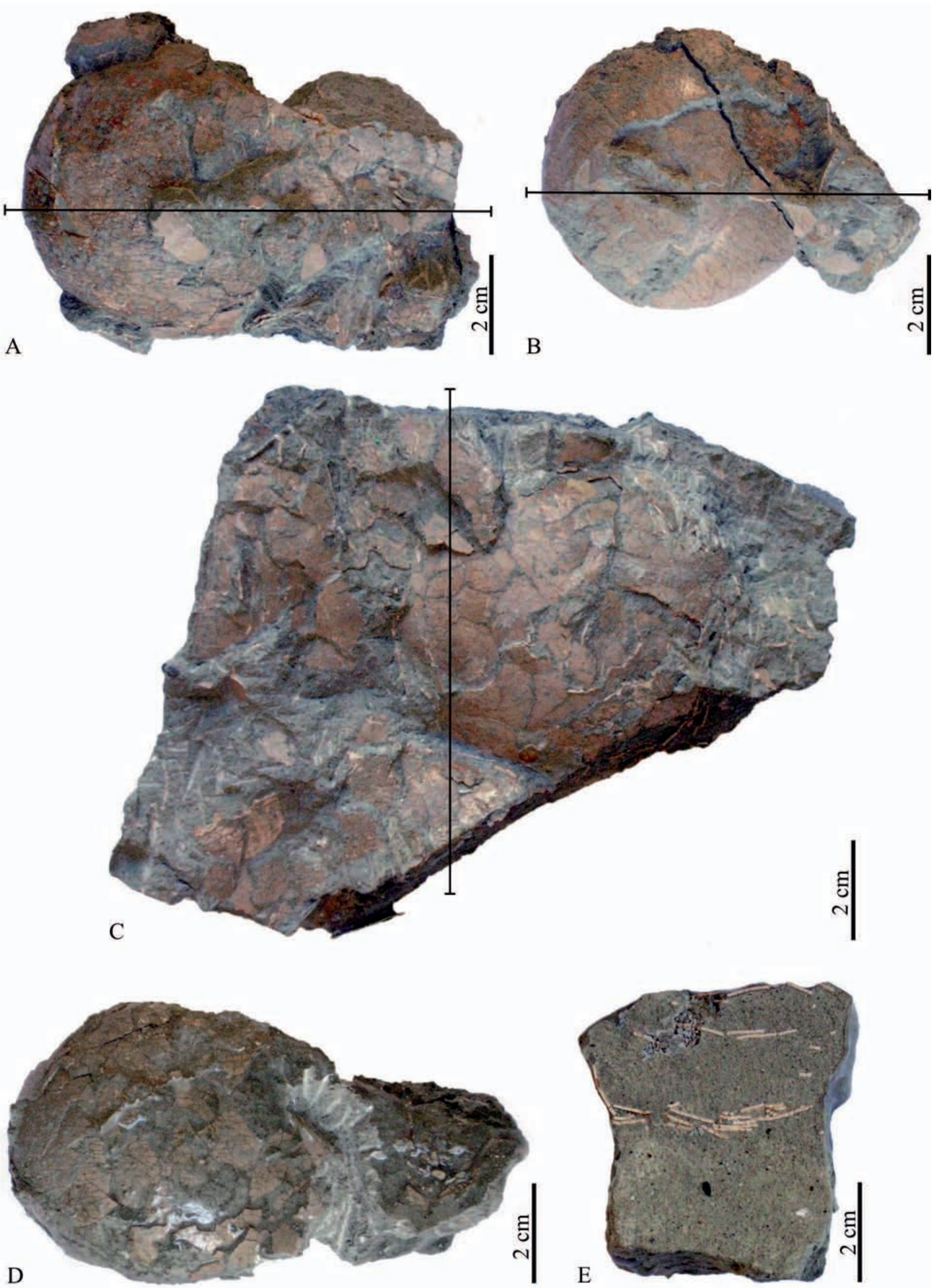
The Apolakkia Formation consists of regular alternations of thinly bedded clays and siltstones, rarely marls, and lignites. Most of these layers commence with a sharp contact with the underlying stratum and have a light greyish colour. Towards the top, the colour gradually changes into a darker grey, which reflects an increase of organic and ferruginous content (Meulenkamp et al. 1972). Many of the horizons have a lateral extent of several square kilometres. Dark-brown, fine- to coarse-grained channel sandstones cut into these beds. The sandstone bodies are usually characterized by an upward decrease in grain size, and may show large-scale cross-stratification in tabular sets or small-scale trough cross-bedding. Often a gradual transition from channel sandstones into the overlying light grey clays or marls can be observed. Meulenkamp et al. (1972) interpreted the depositional environment of the Apolakkia Formation as a low-lying plain with meandering rivers and numerous lakes and swamps.

The fossil eggs were found about 4 km south of the village Apolakkia at a prominent exposure close to the main road (Fig. 1), and approximately 150 m below the contact with the overlying channel sequence (Fig. 2). The clutch was enclosed within a greenish-grey siltstone on top of a channel sequence. This channel filling can be subdivided into several units that usually have erosional contacts on their bases. The sandstones of the channel fillings are poorly sorted, and in the middle of the filling slightly conglomeratic coarse sandstone occurs, having clast sizes up to 35 mm. All channel deposits show weakly developed trough cross stratification or cross stratification in tabular sets. The lithic arkose consist macroscopically of milky-white quartz grains, deep red to purple feldspars and various rock fragments (Fig. 2).

3. Material and methods

Five almost complete eggs and a number of eggshell fragments were recovered from an in-situ clutch (Fig. 3, Table 1). The material is now housed at the Athens Museum of Palaeontology and Geology of the National and Kapodistrian University of Athens (AMPG 515 – AMPG 519). After preparation, the recovered eggs and eggshells were impregnated with Plexigum (Diacon Cmg 302 Clear 011) dissolved in acetone. This was applied onto the external surface of the eggs to prevent destruction of the thin and fragile shell. Examination of the microstructure of the eggshell pieces was undertaken with a stereo-microscope (Leitz Wild M3B), and interpretative drawings of thin sections were made with Camera lucida, and a scanning electron microscope (SEM) at the Department of Geography and Geology, University of Copenhagen. For SEM analysis, the eggshell fragments were ultrasonically cleaned of adhering sediments and coated with gold. In addition, the mineral compositions of the eggshell and the sediment

Fig. 4. The five best-preserved eggs collected at the locality. The thin lines on eggs A-C indicate the sections from the CT scans illustrated in Fig. 6. **A** – Complete egg with associated remains of another crushed specimen (AMPG 515). **B** – Complete, uncrushed specimen, showing the sub-spherical shape of the egg (AMPG 516). **C** – Block with one complete and two partly preserved eggs (AMPG 517). **D** – Partly crushed egg (AMPG 518). **E** – Cross section through a partly crushed specimen. Notice the stacking of eggshell fragments in the bottom of the egg (AMPG 519).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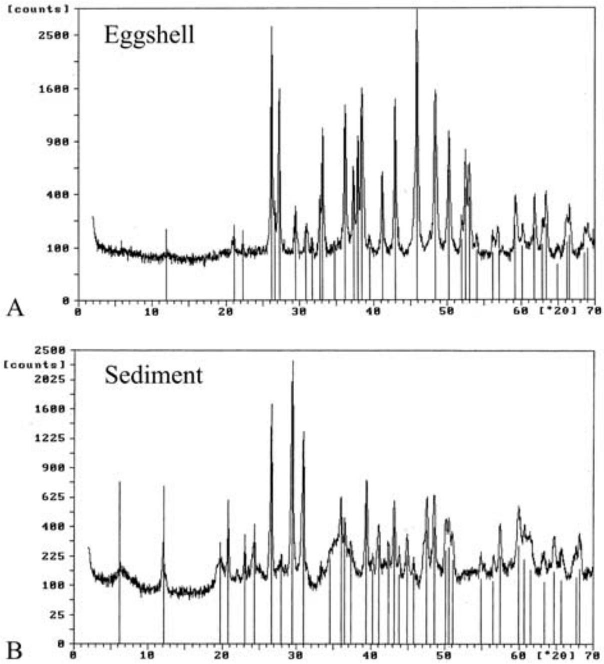

Fig. 5. X-ray diffraction spectres of eggshell and sediment. **A** – The spectre for the sample of the eggshell shows a high content of aragonite, plus minor content of quartz, calcite, serpentinite, and some ferric components. **B** – The spectre for the sediment from the clutch is dominated by quartz and calcite, together with minor amounts of dolomite, serpentinite and clay minerals.

were examined by X-ray diffraction analysis (XRD) at the Department of Geography and Geology, University of Copenhagen. Selected pieces of eggshell were ground to powder (< 45 µm) and analysed by a Philips Analytical X-Ray B.V., provided with a Cu-anode, operated at 40 kV for this procedure. Furthermore, the three best-preserved eggs (AMPG 515 – 517) were investigated by computed tomography (Fig. 6). During the scan the eggs were orientated as close as possible to their original orientation as extracted from the clutch. The CT scans were performed by TOTAL France, and the TC data were subsequently processed using AMIRA software (Advanced 3D visualization and volume modelling, Mercury Computer Systems). In addition to the eggs, ten turtle carapace fragments (AMPG 520 – 529) were studied and identified in hand sample.

4. Systematic palaeontology

Oofamily Testudoolithidae Hirsch, 1996

Type genus: *Testudoolithus* Hirsch, 1996.

Diagnosis (after Hirsch 1996): Eggshell of testudoid basic type and spherurigidis morphotype; calcareous layer with interlocking (rigid) shell units; simple widely spaced pore canals between shell units: spheroidal to ellipsoid egg shape.
Type species: *Testudoolithus rigidus* Hirsch, 1996.

Diagnosis (after Hirsch 1996)**:** Testudoolithidae with spherurigidis morphotype; spheroidal eggs; eggshell thickness 0.2-0.8 mm.

Referred specimens: Five almost complete eggs (AMPG 515 – AMPG 519), from the Pliocene Apolakkia Formation of Rhodes, Greece (Fig. 4), and a number of unnumbered, loose eggshell fragments from the clutch.

4.1. Description of the eggs

The eggs were found in a clutch with a lens- to bowl-shaped cross section. The shape of the clutch was defined by the distribution of the eggs, as there were no visible sediment-differences in- and outside of the supposed nest. Its original diameter was estimated at approximately 30 cm (Fig. 3). The original number of eggs could not be determined as the clutch was only exposed in transverse section. Five eggs were removed for study. Three additional eggs and numerous eggshell fragments became visible behind the removed eggs but were left in-situ at the locality for possible future larger scale excavation of the site. An unknown number of eggs may have already been lost to erosion. Most of the eggs of the clutch appeared complete, but slightly crushed by lithological compaction (Fig. 4). The largest diameter of the sub-spherical eggs measures 53-60 mm with a maximum height of about 40 mm. Their original undeformed diameter is estimated at 45-50 mm. The eggshells are about 0.3-0.5 mm thick (Table 1) and recrystallized (Fig. 6). The smooth external surface of the eggshells has a light red colour. Above the complete eggs was a layer of crushed eggs and eggshell fragments (Fig. 3B). These fragments roughly have 5 mm in diameter and overlap each other in places (Fig. 4).

AMPG 515 is a nearly complete egg, superimposed over the remains of another egg (Fig. 4A). Part of the eggshell was lost during excavation. AMPG 516 is also virtually intact, but lacks the shell in its upper part (Fig. 4B). AMPG 517 is situated within a small sediment block, containing one complete specimen and the remains of two fragmentary eggs (Fig. 4C). AMPG 518 is only one half of an egg (Fig. 4D), whereas the specimen AMPG 519 exposes a cross-section through an egg (Fig. 4E).

4.2. X-ray diffraction analysis

Two samples were analysed: an unnumbered loose eggshell fragment found associated with the collected

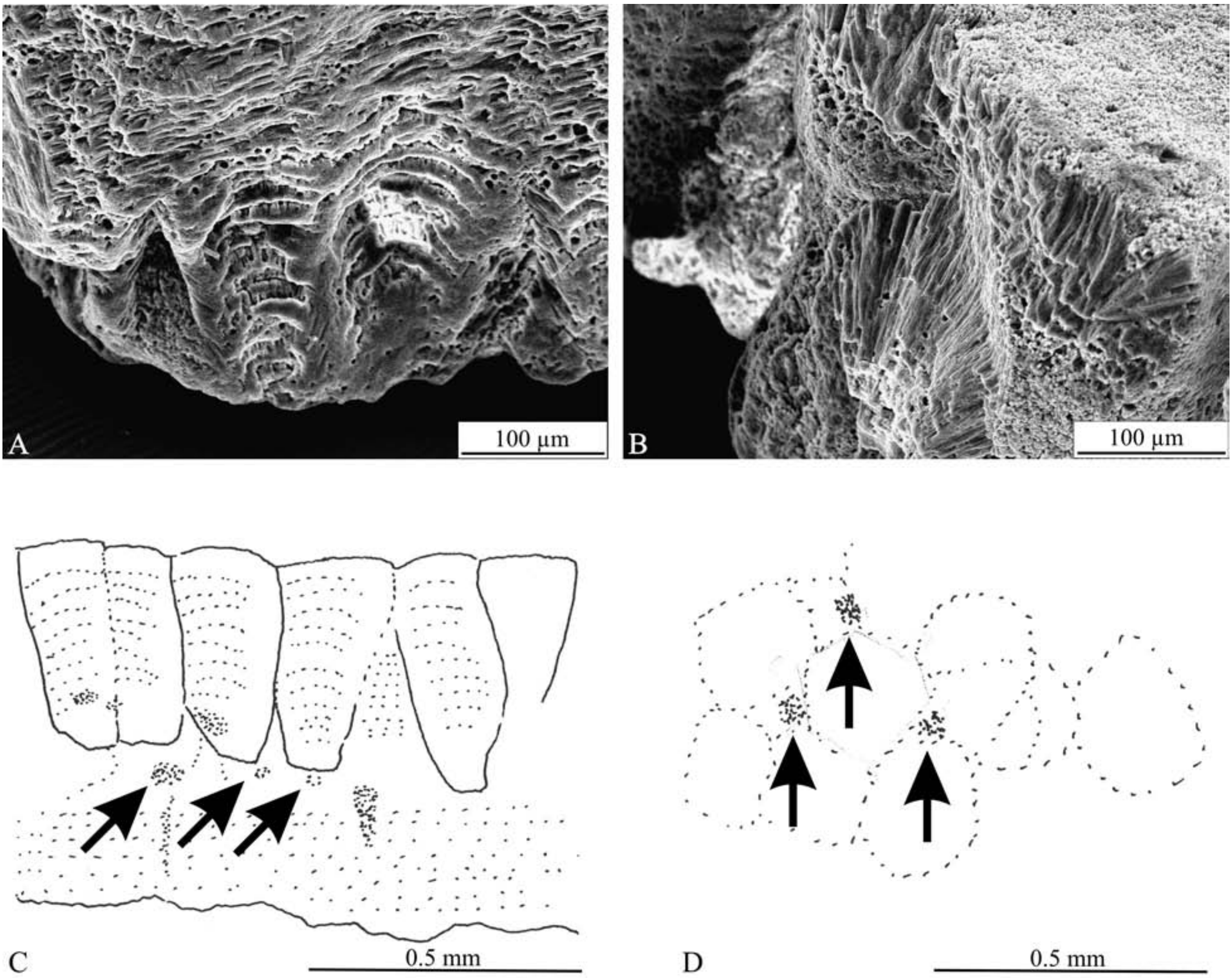

Fig. 6. SEM images of the eggshells. **A** – The eggshell is divided into an outer, crystalline layer composed of fan-shaped, tightly interlocking units, and a partly missing, thin structureless inner layer. **B** – Each crystal unit displays a radial fractured symmetry of aragonite projecting from a nucleation site, located in the surface of the inner layer. **C** – Camera lucida drawing of thin section through the eggshell, showing the outer layer of tightly interlocking crystal units and the structureless inner layer. The remains of a former organic core are visible at the base of each shell unit (arrows). **D** – Camera lucida drawing of a thin section through the surface of the eggshell. The interlocking of the crystal units forms a hexagonal pattern. A few pores can be found located between the shell units (arrows).

eggs, and a sample of the sediment surrounding the eggs. The interpretation of the spectrum for the eggshells showed a high content of aragonite. In addition, quartz, calcite, and serpentinite can be identified in small quantities, together with some ferric components (Fig. 5A). The analysis of the sediment shows quartz and calcite as main components, together with dolomite, serpentinite and clay minerals (Fig. 5B).

4.3. SEM and light microscope analysis

Scanning electron microscopy analysis of eggshell fragments reveals that the eggshells are highly recrystallized, but shell units are composed of radiating spherulites that are on average 0.45 mm high and 0.25 mm wide, can still be recognized (Fig. 6A, C). Further, the eggshell seems to be composed of an outer crystalline layer and an inner amorphous layer, which is partly missing (Fig. 6C). The units display a radial fractured symmetry typical of aragonite, and each unit is projecting from a nucleation centre located on the surface of the inner layer (Fig. 6B).

When examined in thin section under light microscope the shell units are interlocking and compact, without intermediate gaps between nucleation sites. A

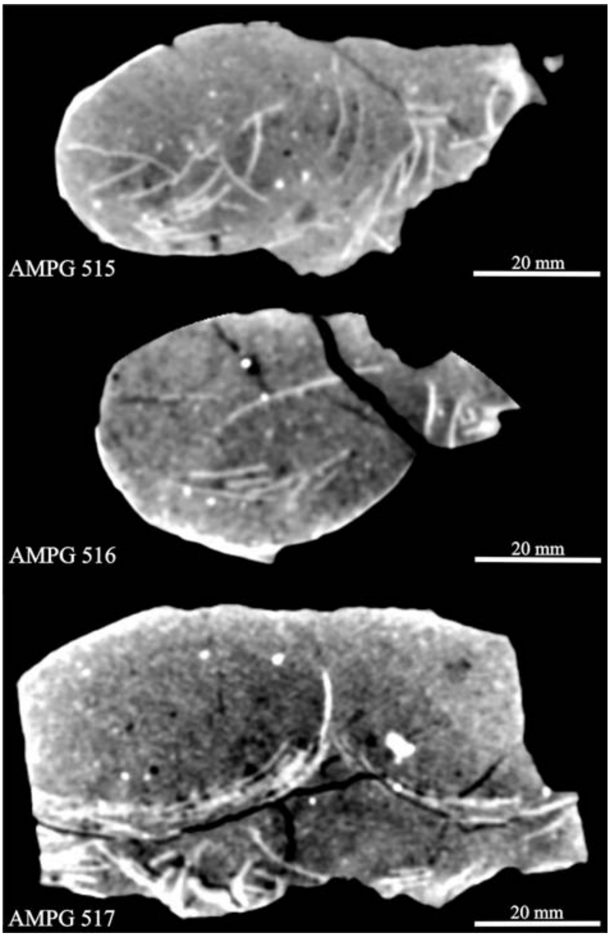

Fig. 7. CT scans of the three best-preserved eggs (AMPG 515-517) show that they contain stacked eggshell fragments in the bottom of the eggs, and no remains of embryonic bones, indicating that the eggs were hatched before further sediment accumulated on top.

former organic core can be identified at the base of each shell unit (Fig. 6C). The external surface of the eggs also reflects the shell unit morphology, which appear round to hexagonal in shape. Only a few pores are visible between the shell units (Fig. 6D).

4.4. Computed Tomography Scanning

Computed tomography (CT) of the three best-preserved eggs (AMPG 515-AMPG 517) revealed a high-density outer region (white) corresponding to the egg-shell. The almost homogenous sediment filling of the inner void of the eggs is of lesser density, and appears grey in the CT-scans (Fig. 7). Single small clasts of higher density appear sporadically in the sediment. AMPG 515 contains shell debris in the lower half of its sedimentary infill (Fig. 7). AMPG 516 shows one large eggshell fragment in the upper half of the egg and a layer of several, smaller eggshell fragments at its base. In addition to a complete egg (AMPG 517), the sediment block reveals fragments of two additional eggs; these occur beneath and adjacent to AMPG 517. Also this egg contains numerous small eggshell fragments in a horizontal layer at its base (Fig. 7).

5. Additional turtle remains from the Apolakkia Formation

In autumn 2007, a small association of turtle carapace fragments (Fig. 8) was discovered eroding from the base of a steep slope near the site of the egg clutch. Although the precise stratigraphical horizon of the chelonian remains has yet to be determined, it is tentatively assumed that the carapace pieces originate from a sandstone bed a few metres below the nest-bearing horizon. The carapace fragments are all small (the largest one having an overall length of less than 25 mm), and based on their thickness, up to 5 mm, they appear to have belonged to a rather small individual. Three of the fragments are identified as partial peripheralia (Fig. 8B) and at least two as pleuralia (Fig. 8A, C). The fragments preserve partial sutural margins, and shallow grooves (some of which may represent boundaries between the dermal scutes) occupy the dorsal and/or ventral faces of the bony elements. Furthermore, the surface of the pleural plates is sculpted by prominent areolae (Fig. 8A).

6. Discussion

Testudoid basic type eggs are characterized by eggshells consisting of shell units composed of a single layer of needle-like, aragonitic crystallites originating from an organic core located on the shell membrane. They can be divided into soft-, pliable-, and rigid-shelled eggs. The latter can be subdivided into two morphotypes (Hirsch 1983, 1996). The spherurigidis morphotype is characterized by shell units higher than wide with interlocking adjacent crystals that form a rigid shell; in the spheruflexibilis morphotype the shell units are generally wider than high and loosely abutting in a flexible shell or tightly abutting in a pliable shell (Hirsch 1996).

The eggs in this study are composed of tightly packed, columnar argonitic crystalline units that are approximately double as high than wide and interlock

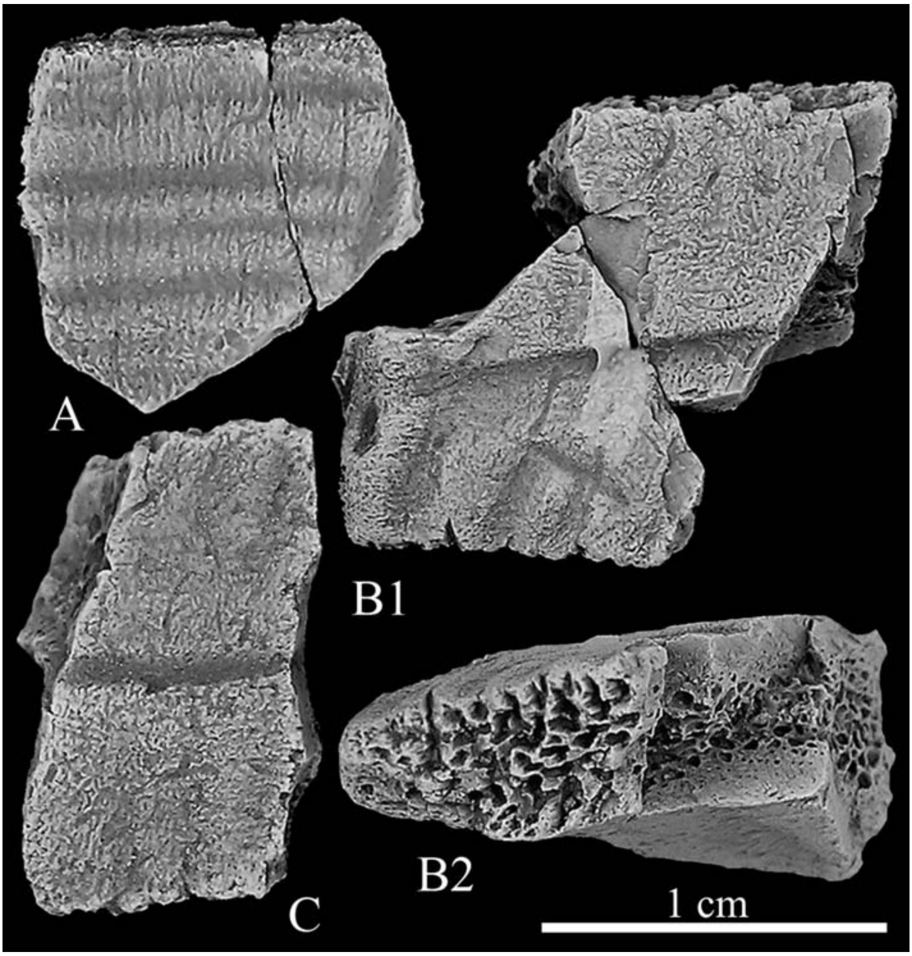

Fig. 8. Turtle carapace fragments from the Apolakkia Formation. **A** – Pleural plate in dorsal view (AMPG 520). Notice the prominent areolae. **B** – Peripheral bone in B1, dorsal and B2, anterior or posterior views, respectively (AMPG 521). **C** – Pleural plate in dorsal view (AMPG 522).

with the adjacent units forming a rigid shell. Pores are located between the shell units. The eggshells are 0.3-0.5 mm thick, and the undeformed shape of the eggs is spherical with an estimated diameter of 45-50 mm. The eggshell microstructure therefore indicates a rigid eggshell. This assigns the eggs from the Apolakkia Formation to the oofamily Testudoolithidae and oogenus *Testudoolithus* Hirsch, 1996 (probably *Testudoolithus rigidus* Hirsch, 1996).

Fossil testudinate eggs are known from the Upper Jurassic of Portugal and Spain (Kohring 1990a, b) and the Cretaceous of England (Hirsch 1983), France (Masse 1989), Spain (Moreno-Azanza et al. 2008), Brazil (Azevedo et al. 2000), North America (Zelenitsky et al. 2008; Knell et al. 2011), Japan (Fukuda & Obata 1991; Isaji et al. 2006), China (Jackson et al. 2008) and Mongolia (Mikhailov et al. 1994). From the Tertiary, fossil eggs of the testudoid basic type have been found in the Western Interior of North America (Hirsch & Bray 1988), Africa (Hirsch 1994), Europe (Hirsch & Lopez-Jurado 1987), Mongolia (Mikhailov 1997), Venezuela (Winkler & Sänches-Villagra 2006), France (Kohring 1993), and the Canary Islands (Hirsch 1996).

The aragonitic eggshell composition identifies the eggs in this study as chelonian, as other vertebrates have eggs with calcitic shells (Hirsch 1983, 1996). The size of the eggs is in the upper range for chelonians

Table 2. List of fossil and Recent Testudinidae from the Greek mainland and islands presented in stratigraphical order from Miocene to Recent forms, with localities and bibliographical references. Turtle taxonomy is that of Bickham et al. (2007a, b).

Taxonomy	Locality	Reference
Miocene		
Lambrochelone nostimiensis gen. et sp. nov.	Nostimo (Kastoria)	Georgalis et al. in press
Testudo sp. I	Chios Island	Paraskevaidis 1955
Testudo sp. II	Chios Island	Paraskevaidis 1955
Testudo amiatae	Thessaloniki	Campana 1917
Testudo amiatae	Allatini (Thessaloniki)	Bachmayer & Symeonidis 1970
Testudo marmorum	Pikermi (Attica)	Gaudry 1862-1867; Bachmayer et al. 1970
medium-sized *Testudo* sp.	"Falaise de Karabouroun" (Thessaloniki)	Arambourg & Piveteau 1929
Testudo marmorum	Halmyropotamos (Euboea)	Melentis 1970
Testudo sp.	"Falaise de Karabouroun" (Thessaloniki)	Arambourg & Piveteau 1929
Testudo spec.indet.(nov.spec.?)	Liossati (Attica)	Bachmayer & Symeonidis 1977
Testudo sp.	Samos	Forsyth Major 1894
cf. *Cheirogaster schafferi*	Samos	Brown 1931; Szalai 1931; de Lapparent de Broin 2002
cf. *Cheirogaster* cf. *schafferi*	Pikermi	Bachmayer 1967a, b; de Lapparent de Broin 2002
cf. *Cheirogaster* sp.	"Ravin de Vatilük" (Thessaloniki)	Arambourg & Piveteau 1929; de Lapparent de Broin 2002
Testudinidae indet.	Serres Basin	Gad 1989
Unpublished Testudinidae	Serres Basin	N. Karystineos, pers. comm.
Pliocene		
Testudo cf. *graeca*	Megalo Emvolo (Thessaloniki)	Bachmayer et al. 1980
large-sized Testudinidae	Megalo Emvolo (Thessaloniki)	Bachmayer et al. 1980
Cheirogaster sp. (size of *C. perpiniana*)	Epanomi (Thessaloniki)	Vlachos 2007
Testudinidae indet.	Silata (Chalkidiki)	Syrides 1990
Testudo sp.	Vatera (Lesvos)	de Vos et al. 2002
cf. *Cheirogaster* aff. *schafferi*	Vatera (Lesvos)	de Lapparent de Broin 2002
Testudo marginata	Lakonia (Peloponnesus) Upper Pliocene/ Lowermost Pleistocene	Schleich 1982
Pleistocene		
Testudo sp.	Potidea (Chalkidiki), Pleistocene?	G. Koufos, pers. com.
Testudo sp.	Xerias (Kavala)	Tsoukala et al. 2010 (in press)
Clemmys caspica	Megalopolis (Peloponnesus)	Melentis 1966
Testudo sp.	Psychiko (Attica)	Bachmayer & Symeonidis 1970
Testudo sp.	Petralona Cave (Chalkidiki)	Sickenberg 1971
Testudo marginata cretensis	Gerani and Zourida caves near Rethymnon	Bachmayer et al. 1975
Testudo marginata	Charkadio Cave (Tilos, Dodecenese)	Bachmayer & Symeonidis 1975
Unpublished Testudinidae	North of Diros coastal cave in South Peloponnesus	G. Theodorou, pers. obs.
Recent		
Testudo graeca ibera	Rhodes, Samos	Ioannides et al. 1994; Ioannides & Dimaki 1995-1996; Werner 1930, 1938
Testudo hermanni boettgeri	Pefka, Rhodes	Broggi 1997; Bader & Riegler 2004
Testudo hermanni	Lesvos Rhodos (?)	Ioannides et al. 1994; Bader et al. 2009
Emys orbicularis	Lesvos	Ioannides et al. 1994
Testudo graeca	Lesvos, Chios, Samos, Kos, Rhodos (?) , Leros, Symi and Kalymnos	Ioannides et al. 1994; Dimaki 2002; Bader et al. 2009
Testudo marginata	Lesvos, Chios, Skyros and Paros, Mt Parnes and Mt Hymettus (Attica), Mt Ossa (Thessaly), Generally in Cyclades (17 islands).	Werner 1930; Ioannides et al. 1994; Clark 1970
Mauremys caspica	Samos, Rhodes and Symi	Ioannides et al. 1994; Dimaki 2002
Trionyx triunguis	Kalymnos, Leros, Kos and Rhodes	Dimaki 2002
Clemmys caspica rivulata	Rhodes, Naxos, Linaria, Skyros, Lemnos	Frazer 1965; Werner 1930; Wettstein 1953, 1957
T. hermani, T. marginata, T. graeca	Greece (42 localities)	Hailey & Willemsen 2003
Testudo ibera	Lemnos	Werner 1930

and is only reached by certain sea turtles (e.g. *Caretta caretta* ,*Chelonia mydas*) and large land tortoises, genus *Geochelone* and *Chelonoides* (Chen & Cheng 1995). A comparison with the eggshells from *Geochelone elephantopus ephippium* (cf. Krampitz et al. 1972) shows almost no structural differences.

The CT-scans revealed no embryonic material within the eggs but instead showed numerous eggshell fragments aligned in a manner Mueller-Töwe et al. (2002) considered typical for eggs that were filled with sediment during the hatching process. This indicates that the eggs were hatched successfully.

Although chelonian remains are unknown from Rhodes, the fossil record of Greek tortoises show that giant tortoises existed in Greece from Miocene to Pliocene times (Table 2). However, the taxonomy of the Pliocene tortoises of Greece is still uncertain. Some giant specimens are described only at genus level and for some others more work is needed (de Lapparent de Broin 2001: cf. *Cheirogaster* aff. *schafferi* from Vatera). Furthermore, it is not possible to confidently assign the carapace fragments collected near the egg site to any known chelonian taxon. However, the prominent sculpting of the areolae (Fig. 8A) and the rounded edges of the free peripheralia (Fig. 8B) indicate that they belong to a continental form. The small dimensions of the carapace fragments suggest that they belonged to a smaller specimen than the one that laid the eggs.

7. Conclusions

Five eggs from an in-situ egg clutch are described from the Pliocene Apolakkia Formation of Rhodes, Greece. Based on shape, mineralogy, dimensions, and micro- and ultrastructure, the eggs are identified as chelonian eggs of the testudoid basic type and can probably be assigned to the oospecies *Testudoolithus rigidus* Hirsch, 1996. Computerized Tomography scanning of complete specimens revealed the eggs to contain horizontally aligned eggshell fragments and no embryonic material, indicating the eggs to be hatched. The palaeoenvironment and depositional scenario for the Apolakkia Formation, together with the size of the eggs and their microstructure, suggests that the eggs were produced by giant land tortoises. The carapace fragments found nearby further confirms the presence of terrestrial tortoises in the Apolakkia Formation. The above described egg and carapace fragments are the first record of chelonians, and reptiles in general, from the Apolakkia Formation.

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