Tusk Paleoohistology as a Tool in the Discrimination of Fossil Tusks from Greece

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INTRODUCTION

The aim of this study is to compare the dwarf elephant tusks, found on the island of Tilos, to those of *Elephas antiquus* and *Mammuthus meridionalis*, in respect to the dentine's histological characteristics. In the past, Proboscidean tusk dentine has been used to distinguish tusks and tusk fragments of different taxa (Espinoza & Mann, 1993; Fisher et al., 1998; Palombo & Villa, 2001; Palombo, 2003). For the most part though, these examinations included only the Schreger angle. On previous papers (Agiadi, 2001; Theodorou & Agiadi, 2001; Agiadi, 2003), we have examined other histological features, namely the dentinal tubule's size and density. At the same time, Trapani & Fisher (2003) used the Schreger Pattern's angle, wavelength, and qualitative appearance, to distinguish between tusks of mammoths (*M. primigenius* and *M. columbi*) undifferentiated), mammoths (*Mammuthus americanum*) and extant elephants (*Elephas maximus* and *Loxodonta africana*). In the current study, we examine for the first time all the above features in conjunction, in order to discriminate between tusks of *Elephas antiquus* and *Mammuthus meridionalis*, the two Proboscidean taxa, which dominated the Greek Peninsula during the Quaternary. Furthermore, we compare the obtained results to the corresponding ones for the dwarf elephant tusks from the Tilos Island. Specifically, the characteristics examined herein (Fig. 1) are: the Schreger angle (α), the Schreger Pattern's phenomenon wavelength (λ), the Schreger Pattern's qualitative appearance (q), the dentinal tubule density (dtd) and the dentinal tubule diameter (dtd).

The material used for the present study (Table 1) consists of: 1) two tusks from the Lower Pleistocene locality of Vlachioti (Lakonia, Peloponnisos, Greece), which have been attributed to *Mammuthus (Archidiskodon) meridionalis*, by identification of other skeletal and dental material (Symeonidis & Theodorou, 1986), 2) one tusk found near the village Nissoi (Ilea, Peloponnisos, Greece) by Associate Prof. Theodorou during a field trip to the area on July 1994. According to Assoc. Prof. Theodorou, this specimen exhibits the typical features of *Elephas antiquus* and is consequently attributed to this species (data under publication), 3) five tusks from the area of Megalopolis (Arcadia, Pelopo-
nnisos, Greece) identified by Melentis (1961) as belonging to Elephas (Palaeoloxodon) antiquus, 4) two tusk pieces also from Megalopolis (Melentis, 1961), which belong to Mammuthus meridionalis, and 5) fourteen tusks and tusk pieces found in the Charkadio Cave (Tilos, Dodecanese islands, Greece). It has been noted by previous studies (Theodorou, 1983), that no proof of any interaction between the dwarf elephants from Tilos islands and the dwarfs from Malta has been provided to date. Consequently, the two endemic evolutionary phenomena have progress separately. However the fossil elephant material found on the island of Tilos is still provisionally attributed to Palaeoloxodon antiquus falconeri (Theodorou, 1983).

Concerning methodology, the structure of the tusks' dentine was observed by combination of mesoscopic and microscopic investigation. The features were observed in detail using an optical petrographic and a scanning electron microscope (S.E.M.), under various magnifications. For this purpose, transverse sections were cut and thin sections were prepared whenever necessary. Our observations mainly concerned the perpen-
picular plane to the tusks' axes, since this is the direction
were the Schreger Pattern appears. Only stub samples
examined under the S.E.M. were orientated parallel to
the tusks' long axes and outer surfaces (circumferential
plane), so that we could measure the dentinal tubules' density and diameter. Occasionally, we also examined
stubs on the radial direction, in order to see the longitudinal
sections of the dentinal tubules.

In order to evaluate the Schreger Pattern's characteristics, on our samples, pieces of the tusks were
encased in polyester resin. The blocks were cut perpendicularly
to the tusks' axes and were then polished
throughly with emery dust of two sizes. Afterwards the
polished surfaces were scanned and the $a_s$ was measured
at high magnification, using image processing software.
In particular, the program CorelDraw vs.10 was
used for this purpose. The scanned pictures were
processed to enhance the Schreger lines. Then, under
magnification, the tangents were drawn on each side of
the angle. The $a_s$ was measured on the printouts. For the
purpose of measuring the $w$ and to characterize the $q$,
thin sections were cut, using the same encased frag­
ments. We must note, at this point, that the classification
of the Schreger Pattern's qualitative appearance follows
here the categories proposed by Trapani & Fisher (2003).
In particular, these authors separated three main cate-
gories, "V", "C", and "X". When we observe a transverse
section of the tusk, i.e. perpendicular to the growth
surfaces, the "V" pattern occurs when there are continuous
lines, oblique to the incremental features, with one direction
dextral or sinistral, being locally dominant. The "C"
pattern consists of rectangular light and dark areas
resembling a checkerboard. The diagonally neighbouring
dark or light areas may share only a corner, or may be
more broadly confluent. Finally, the "X" pattern is
described as having criss-crossing continuous lines,
within the incremental features and occurring in both
dextral and sinistral direction [Trapani & Fisher, 2003].

**ABBREVIATIONS**

- $sa$ Schreger angles
- $w$ Schreger Pattern's phenomenon wavelength
- $q$ Schreger Pattern's qualitative appearance
- $dtd$ dentinal tubule density
- $tdi$ dentinal tubule diameter
- S.E.M. Scanning Electron Microscope
- S.P. Schreger Pattern
- CDJ cementum-dentin

Fig. 2. According to Trapani & Fisher (2003), there are three categories of qualitative appearance that can be used to classify the Schreger Pattern. The "V" pattern consists of "continuous lines, oblique to the incremental lines, with one direction locally dominating". "Rectangular light and dark areas resembling a checkerboard, with the diagonally neighboring dark or light areas sharing only corners", result in the "C" type of Schreger Pattern. If however the Pattern is made of "criss-crossing continuous lines, oblique to the growth increments, occurring in both dextral and sinistral directions", then we place this to the "X" category. We can also distinguish the intermediate categories "XIC", "VIC", and "XIV".
(a) Transverse section on a tusk piece of Mammutthus meridionalis from Vlachioti (Lakonia). We can see that the dominant feature is "XIC".
(b) Transverse section on a tusk piece of Elephas antiquus from Nissos (Evia), where we can observe mostly "V", and rarely "X" patterns.
(c) Transverse section on a tusk piece from a dwarf elephant (Elles, Dodokanasi). On the outer zone of the Pattern, we can clearly observe the "C" type, which changes to "V" towards the pulp cavity. The "X" type can be seen only on the inner zone.

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**FOSSIL TUSKS FROM GREECE**

3
**Tusk Paleohistology**

Proboscidan tusks are enlarged incisors formed by orthodentine, which is covered on the outer surface by a thin layer of cellular cementum. Enamel, in the species examined here, is found only as a very thin layer, covering the tip of the tusks. Due to the special functions and the consequent enlargement of tusks, the dentine has formed certain features, unique to Proboscidean tusks, which combine to produce the Schreger Pattern (S.P.). This Pattern was first observed, by Bernard Schreger (1800), on sections perpendicular to the tusk's axis. It consists of two sets of light and dark lines, radiating from the outer dentine surface, towards the axis of the tusk, in a spiral fashion. One set of Schreger lines radiates clockwise and the other counter-clockwise, thus intersecting to form the Schreger angles.

The Schreger Pattern (Fig. 1a) is the macroscopic manifestation of the microscopic architecture of tusk dentine. During odontogenesis, as the odontoblasts move towards the proximocentral part of the tusk's pulp cavity, they leave behind them the dentinal tubules, which are the traces of the odontoblasts' sinusoidal movement (Raubenheimer et al., 1998). As a result, when observing a transverse section of the tusk, we can essentially observe the undulation of the dentinal tubules, projected as the dark and light lines of the Schreger Pattern (Figs. 1 & 2). Dark lines correspond to the concave part of the undulation, while the light lines represent the convex part. The fact that, on a transverse section, we do not observe alternating light and dark concentric rings, but rather the dextral and sinistral Schreger lines, leads to the conclusion that the periodic movement of the odontoblasts, towards the proximocentral part of the pulp cavity, does not occur simultaneously for the entire band of odontoblastic cells. On the contrary, the cells are organized in bundles that move simultaneously, producing sets of dentinal tubules, which are in phase with each other, but have a phase difference of π, in relation to the neighbouring sets.

In respect to all the above, the parameters characterizing the Schreger Pattern are the size and density of the dentinal tubules, the wavelength of their undulation, and the size of the dentinal tubule sets. These parameters are defined by the shape of the original pulp cavity; the size and density of the odontoblasts and the rate of dentine deposition, which in turn produce the final shape and size of the tusk. On the circumferential view of the tusk, we can directly measure the size and density of the dentinal tubules. Also, on a transverse section of the tusk, we measure the Schreger Pattern phenomenon wavelength, as the distance between two adjacent dark or light lines. As for the size of the dentinal tubule sets, this is expressed instead by the Schreger angles, which we also measure on transverse sections.

**Observations**

*Mammuthus meridionalis*

The Schreger Pattern on *M. meridionalis*, as observed on the transversal plane, appears continuously throughout the thickness of the tusk's dentine. The *sa* decreases from the outermost surface of the dentine towards the pulp cavity. Measurements of the *sa*, on the outer approximate 45% of the dentine's thickness, give values between 83° - 128°, with the maximum value appearing at 15%. Fig. 3c shows the relationship between the *sa* values and the distance from the outer dentine surface. There are four areas of deviation, from the general decrease of the *sa*, namely at: 13.6-19.1% (maximum value of *sa* at 16.4%), 21.6-23.6% (max at 22.7%), 26.4-28.2% (max at 27.5%), and 40%-48.2% (max at 43.6%). Regarding the *w*, measurements were made at the same area as the *sa* and produced values between 0.55-0.95 mm. Qualitatively the Schreger Pattern exhibits mostly "X" patterns and occasionally "C" patterns, as those were described by Trapani.
& Fisher (2003) (Fig. 2a). We are not able to distinguish any "V" patterns, although our examination does not include the inner part of the tusk's thickness, where the above authors mention the appearance of the "V" pattern on the tusks of *M. primigenius* and *M. columbi*.

On the microscopic level, we observe the organization of the dentinal tubules (Fig. 4a & b), and measure their *tdi* and *did*, near the cementum-dentine junction (CDJ), but below the mantle dentine. Due to the sinusoidal movement of the odontoblasts, the dentinal tubule sections, on a circumferential view of the tusk's dentine, are ellipses with their diameters around the direction of the tusk's axis. Thus the large diameter of an elliptical section is a phenomenon diameter of the tubule. Additionally, the lateral component of the odontoblasts' movement is relatively small, and it varies amongst adjacent tubules in a sinuous fashion. Consequently, calculating the mean tubule small diameter, for an area of about 11 \( \times 10^4 \) mm\(^2\), should eliminate the fluctuation due to the lateral movement. As a result we accept this mean value as the true dentinal tubule diameter (*ldi*). For the samples of *Mammuthus meridionalis* the measurement of the dentinal tubule small diameter produces values between 1.0-2.0\( \mu \)m. On the same circumferential microscopic views, we also measured the *dld*, which ranges from 25500 to 43000 dt/mm\(^2\). Both the *tdi* and *ldi* was measured on a total of 20 samples.

**Elephas antiquus**

The tusks of *E. antiquus* from both localities exhibited the same microstructural features. The *sa* decreases from the outer part of the dentine towards the pulp cavity. Measurements of the *sa* were taken only within the outer 15% of the dentine's thickness (Fig. 3b), because our tusk samples did not allow for the separation of a larger piece. The *sa* ranges between 131° - 158°, reaching a maximum at 5.8% of the dentine's thickness, which also constitutes an irregularity in the general decrease of the *sa* toward the central tusk axis. It is important to note, at this point, that the *sa* was measured in our samples only in relation to the distance from the cementum-dentine junction, because we have previously established that there is no particular pattern of a *sa* variation along the proximodistal direction, i.e. the Schreger Pattern does not change with the age of the tusk, but rather depends on the shape of the pulp cavity (Theodorou & Agiadi, 2001). This allows us to use tusk fragments even though their position along the tusk was not always known. Qualitatively, the Schreger Pattern exhibits mostly "V" and some "X" patterns. In addition, the *w* ranges between 0.56-0.92 mm, increasing towards the pulp cavity.

Regarding the dentinal tubules' size and distribution (Figs. 4c & 5a), we measure the *ldd* on stubs taken from both the areas near the cementum-dentine and the pulp-dentine junction. There does not appear to be any significant differentiation of this characteristic, among the two areas. In particular, the *ldd* measures between 18300-40365 dt/mm\(^2\). Furthermore we measure the mean dentinal tubule small diameter, which is the true dentinal tubule diameter (*ldi*), at the same areas, to range between 0.5-1.0\( \mu \)m. The total number of samples examined for *tdi* and *ldi* was 18.

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**Fig. 4. S.E.M. images of tusk dentine, showing the distribution of the dentinal tubules.**

(a) Tusk specimen of *Mammuthus meridionalis* from Vlachioti (Lakonia), where a stub has been taken at a distance of about 7.0 mm from the CDJ. We can see the transverse sections of the dentinal tubules.

(b) On the same specimen, we have a radial view of the dentine, where we can see the longitudinal sections of the undulating dentinal tubules.

(c) Tusk specimen of *Elephas antiquus* (1960/183), stub taken from the outer dentine layers, at about 9.5 mm from the CDJ. We observe oblique sections of the dentinal tubules, at a view almost parallel to a growth surface.

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**Fig. 4. Imatges SEM de la dentina de les defences, mostrant la distribució dels tòbuls de dentina.**

(a) Mostra de defensa de *Mammuthus meridionalis* de Vlachioti (Lakonia), on s'ha agafat una peça a una distància de 7.0 mm del CDJ. Podem veure les seccions transverses dels tòbuls de dentina.

(b) Al mateix exemplar, tenim una vista radial de la dentina, on es poden veure les seccions longitudinals dels tòbuls de dentina evolutius.

(c) Mostra de defensa d'*Elephas antiquus* (1960/183), peça agafada a les capes de dentina exterior, a unes 9.5 mm del CDJ. Observem seccions obliques dels tòbuls de dentina, en norma quasi paral·lela a la superfície de creixement.
Dwarf elephants from Tilos island

On the transverse sections of the Tilos elephant tusks, we can clearly distinguish two zones of dentine, with obvious differences in the Schreger Pattern's qualitative and quantitative characteristics. The qualitative appearance exhibits a combination of "V" and "C" patterns on the outer zone, with "C" patterns dominating as we move towards the CDJ. The "X" type of Schreger Pattern is confined to the inner zone, where we sometimes also observe the "V" type. We concentrate on the Schreger angle variance regarding the outer zone, so that our results would be comparable to our measurements on the samples of the other species. To this end, we examined approximately the outermost 50% of the dentine's thickness. Our sa values for this show a range from 108° to 158°. By plotting the sa against the distance from the CDJ, on the specimen T.00/144, we confirm its decrease toward the tusk's axis. However, there is an anomaly, between 26-36% of the dentine's thickness, with a maximum being achieved at about 31% (Fig, 3a). Finally, on the same areas, we also measured the iw, which varies between 0.47-0.67 mm, increasing towards the pulp cavity.

Microscopically, the dtd on our samples has a range from 11524 to 45500dt/mm², and the tdi varies between 2.1-2.9µm (Fig. 5b & c). We examined 13 stub samples from the tusks, each time noting their position on the specimen. There is no differentiation of the size and density values, along the periphery of the tusks, or across the radial, although the greatest density values (dtd > 35000dt/mm²) can indeed be measured on the outermost part of the dentine. However this can be explained by the existence of the mantle dentine, which is characterized by an extreme branching of the tubules.

**DISCUSSION**

In the present study, we have reached valuable results, which further our understanding of the Schreger Pattern. The Schreger angle is related to the phenomenon wavelength and the width of the dentinal tubule sets, in a given position in the tusk (Fig. 1b). The sa increases towards the CDJ and so does the sets' width, but the wavelength decreases. Although we have not examined the relationship between the Pattern's wavelength and the distance from the CDJ, we expect it to be similar to that observed between the angle and the CDJ distance. Such a pattern would be able to differentiate between taxa in the similar manner. However, simply comparing the range of the wavelength, in a given part of the tusks' thickness, does not provide any discrimination. Regarding the Schreger Pattern's qualitative appearance, this depends on how abrupt the boundaries of the tubule sets are. When they are very abrupt, we observe the "C" pattern. When the boundaries on direction are abrupt, and on the other smooth, they produce the "V" pattern. And finally, smooth boundaries, i.e. progressive transmission of the proximocentral movement of the odontoblasts, produce the "X" type of pattern.
<table>
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<th>Locality</th>
<th>Taxon</th>
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<th>d1 (cm)</th>
<th>d2 (cm)</th>
<th>Specimen</th>
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<td>17.46</td>
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Table 1. Tusk material examined in this study, including macroscopic measurements. 1: tusk or tusk piece's length following the proximodistal direction in a straight line, d1: maximum diameter at approximately the middle of the tusk's length, d2: minimum diameter at the same position. The measurements followed by "*" have been taken at the proximal end of the tusk. All of the specimens are deposited in the Museum of Palaeontology and Geology of the University of Athens.

Very important also are the microstructural observations, which once more present the uniqueness of the tusk dentine tissue. Concerning the microstructural features of dentine, the dentinal tubule density does not present any discriminating power, in the samples examined herein. Besides, the tissue is the same in all three taxa, and would be expected to have the same needs in intratubular material (odontoblastic material, neural fibers, etc.). In addition, there appears to be no variance in density amongst different areas of the dentine's thickness, a fact also expected for the same reasons. The dentinal tubule's branching process, in this case, compensates for the increased periphery of the tusk, as we move toward the outer part. However, the dentinal tubule size differs between our samples. In particular, the tusks of the dwarf elephants from Tilos Island have much larger tubules, than the samples of Elephas antiquus and Mammuthus meridionalis. The reasons for this differentiation are not yet clear to us. Although the fossilization processes could have affected this feature, a low degree of calcification, in the first place, may account for the larger tubule diameter found in the tusks of the dwarfs. In such a case, we should think that the smaller and lighter tusks of the dwarf elephants have less need for solidity and resistance to stress than do the ones of larger animals.

Comparing the results for the tusks from the three taxa (Table 2), distinction of mammoths from elephants is clear, by means of the Schreger angle and qualitative appearance, as well as the dentinal tubule diameter. Discriminating however, between the mainland Elephas antiquus from the endemic elephants of Tilos Island, is more difficult. We measured an important difference in the dentinal tubules' diameter, which is much larger than the dwarf elephant tusks. Additionally, we were able to find a slight variance in the Schreger Pattern, in reference to its qualitative appearance. In particular, the dwarf elephant tusks exhibit the "V" and "C" patterns on
the outer dentine zone ("C" being dominant towards the CD), and the inner zone has mostly "X" patterns, while the E. antiquus tusks have "V" and "X" motifs on the outer part of the Schreger Pattern. We cannot provide a definite explanation for this difference. It may be caused by an alteration in the odontogenetic process. However, changes in the entire appearance of the Schreger Pattern, due to mechanical or chemical alterations, without the simultaneous deformation of the entire tusk, have been mentioned before as a result of the fossilization processes (Agiadi, 2003).

To present, archaeologists have always accepted Asia and Africa as the only source of ivory for the ancient Greeks (Hayward, 1990). However, considering the wealth of Proboscidean tusk findings in many continental and island localities of Greece, fossil ivory should be considered as an alternative source. In particular, tusks of the Pleistocene and Holocene endemic and continental species (i.e. E. antiquus, M. meridionalis and the dwarf elephants from the Aegean islands) could provide usable ivory. In fact, fossilization would have progressed on these tusks for only a small period of time. Consequently, any alteration of the chemical and structural properties of this ivory may not be severe, by the time the tusks would have to be cut, curved and processed in order to be used. Therefore, the distinction of ivory from different elephant species becomes greatly important in the assessment of such artefacts' true archaeological value. Perhaps some of the archaeological specimens, which are at present thought to be the product of Mediterranean sea trade may, after thorough examination with the above methodology, turn out to have domestic origin. To this end, we propose the review of the ivory specimens found on Greek archaeological sites, examining all the mesoscopic and microscopic features explained in this study, and the comparison of these specimens with paleontologically identified tusks of known origin.

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REFERENCES