Remains of straight-tusked elephant, *Elephas (Palaeoloxodon) antiquus*
Falc. & Caut. (1847) ESR-dated to oxygen isotope Stage 6 from Grevena
(W. Macedonia, Greece)

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**KEYWORDS** – Mammalia, Elephant, Elephas (Palaeoloxodon) antiquus, ESR-dating, Refugium, Pleistocene, Greece.

**ABSTRACT** – A partial skeleton of straight-tusked elephant, *Elephas (Palaeoloxodon) antiquus*, was excavated from Pleistocene deposits at Grevena, western Macedonia, in 1992-95. The skeleton includes substantial portions of the skull and vertebral column, and represents a large, adult male of about 40 years. Additional remains include fragments of at least one other individual of *E. (P) antiquus* and a large bovid cf. Bos primigenius. Three samples of elephant tooth enamel were ESR-dated (by Y. Bassiakos), giving an age in the range 160-170 kyr BP, i.e. Oxygen Isotope Stage 6. This indicates Greece as a refuge for temperate, woodland-adapted large mammal species at a time when they were largely excluded from northern and central Europe.

**INTRODUCTION AND HISTORICAL OVERVIEW**

The excavated area, in which the elephant was discovered, is situated on the outskirts of Grevena town, which is the metropolitan centre of Grevena Prefecture in western Macedonia, 190 km from Thessaloniki. The broader Grevena basin is situated close to the Pindos mountain and to the river Aliakmon, in whose deposits many riverine fossils have been found (Text-fig. 1). The elephant was found at Ambelia, 585 m above sea level (Text-fig. 2). The area continues to be the source of Plio-Pleistocene fossils, the most recent findings (1997), from the new locality of Milia (Text-fig. 1) comprising proboscidean remains referred to *Stegodon* sp., and including the longest proboscidean tusks ever found in Greece (4.39 m).

In the early 1980’s, a student from Grevena, D. Zisopoulos, discovered elephant remains in an old stream in a building plot close to his house (Text-fig. 2). Research started in 1990, and after preliminary visits for reconnaissance, three substantial field seasons, in 1992, 1994 and 1995 were devoted to excavation of the site. These resulted in abundant elephant remains, very largely pertaining to a single skeleton. The material was found in unconsolidated sands, close to the surface, so the remains are in a rather poor state of preservation, partly because of groundwater percolation, but mainly because of the roots of plants which penetrated the fossils and resulted in great damage. Very few bones, mainly the metapodials, were well preserved. Only two other fossils, teeth of a large bovid, were found in association with the elephant material. The excavations, and the dating project (undertaken in 1996 in collaboration with the Laboratory of Archaeometry of the Nuclear Centre for Scientific Research (NCSR) “Demokritos” (Artiki)), were financed by the Grevena Prefecture, and the material is stored in a municipal building in the town.

**GEOLOGICAL CONTEXT AND EXCAVATION**

**GEOLOGICAL CONTEXT**

A major earthquake (Ms=6.6), followed by a sequence of aftershocks, occurred in the Grevena area on 13th May 1995, and resulted in extensive geological investigations (Pavlides et al., 1995, Mountrakis et al., 1996).

The lithostratigraphic column of the Grevena basin (Savoyat & Monopolis, 1972; Mountrakis et
(Aquitanian) is represented by consolidated, mainly ophiolitic, conglomerates and coarse sandstones (3), while the Early-Middle Miocene is mainly represented by blue-gray pelites-clay stones (4) followed by conglomerates alternating with marls, sandstones and sandy marls (5). (e) The Pliocene-Quaternary deposits consist of Pliocene lacustrine deposits (6), followed by a Plio-Pleistocene, mainly fluvial, sequence (7) of clastic deposits, mainly sands, gravels, conglomerates, with sandstone intercalation and silty lenses. The (MN17) clastic deposits are well known from the Dafnera locality in the north-east of the Grevena basin (Text-fig. 1), where they have yielded a rich Middle Villafranchian vertebrate assemblage (Koufos et al. 1991) in an argillaceous lens (DFN, Text-fig. 3). The fauna is characterized by high percentage (38%) of carnivores, with 44% artiodactyls (Koufos, 1993; Kostopoulos & Koufos, 1994; in press). The presence of giraffoids and large stenonoid horses (Koufos & Kostopoulos, 1993) and the slight predominance of bovids over cervids, argue for an open-savanna like environment.

At the Ambelia locality (Text-figs. 1 and 2), the fluvio-lacustrine Grevena Bed, where the elephant remains were found, consists of dark loose conglomerates alternating with sands, pebbles and gravels with cross-bedding and intense rubification from the regional ophiolites (Text-fig. 4). The dimensions of the clasts range mainly from a few millimeters to one centimeter and rarely up to two centimeters. The wedging of the formation to the southern part of the excavation produced a thickness range from zero to several meters to the north. The main excavation took
plants to penetrate the bones, resulting in some of them being destroyed.

The Holocene consists of cones of debris and talus deposits (8), old fluvial terraces (9) and recent and alluvial fluvial deposits.

EXCAVATION OF THE SITE

The Ambelia site was excavated horizontally in squares of 2m² area. All finds were logged with x, y and z co-ordinates relative to an external zero point to the east of the excavation. For long specimens, angle of dip was also measured. The bones were mostly found in dry sand and were exposed using brushes. The bones were in friable condition and quantities of preservative were required in the field, as well as plaster moulds for lifting. A stratigraphic section was prepared at the west end of the excavation (Text-fig. 4), and sediment samples removed from it for any future research. Site plans for the three years' excavations are shown in Text-figs. 5-7, and a complete reconstruction in Text-fig. 8.

DESCRIPTION OF REMAINS

Order PROBOSCIDEA Illiger, 1811
Family ELEPHANTIDAE Gray, 1821
Genus ELEPHAS L., 1758
Subgenus PALAEOLOXODON (Matsumoto, 1924) ELEPHAS (PALAEOLOXODON) ANTIQUUS (Falconer & Cautley, 1845)

SKULL

The skull (GRE 150, Pl. 1) was badly preserved, but shows characters of taxonomic importance. It comprises the almost complete premolarial tusk alveoli except for some ventral breakage, the left zygomatic arch (squamosal and jugal bones), and some very damaged remnants of the maxillary and basicranial regions. The entire cranial dome (frontal and parietal bones) and occipital portion of the skull were completely eroded away, and are missing. This type of preservation, with predominantly the tusk alveoli remaining, is common in Quaternary elephant skulls (e.g. Lister et al., 1990; Goren-Inbar et al., 1994).

The taxonomically diagnostic part of the skull is the form of the tusk alveoli: very broadly divergent from the midline, directed forward as well as downward, and joined to each other across the midline by a broad, horizontal, triangular flap of bone. This form is characteristic of E. (P) antiquus (e.g. Osborn, 1942), and differs markedly from Mammuthus, where the tusk alveoli are closer together, largely downward-pointing, and sub-parallel to the midline (Lister, 1996a). Measurements of the Grevena skull, in comparison with other European E. (P) antiquus skulls, are given in Table 1. The large size of the specimen, especially the wide tusk alveoli, argue for an adult male.

Text-fig. 3 - Lithostratigraphic column of Grevena basin (Mountrakis et al., 1996), including fossil record.

Text-fig. 4 - Diagrammatic section at the west face of the elephant site. 1) conglomerate, 2) partially consolidated silty sand, 3) Grevena Bed: alternating conglomerates and dark loose sands, 4) silty sand with mica, 5) soil.
Text-fig. 5 - Grevena elephant site: excavation of 1992.
Text-fig. 6 - Grevena elephant site: excavation of 1994.
Mandible

The mandible (GRE 151, Pl. 1, fig. 1; Pl. 2), was found in an overturned position. In contrast to the skull, it was well-preserved, including coronoid processes and articular condyles. The right molar is preserved in place, but the left molar has been lost. Measurements are given in Table 1.

Lower Dentition

The right molar in place in the jaw (Pl. 2) appears to be the M3, on the basis of its large size, tapering rear end, absence of a germinal tooth behind, and probable plate count. Ten enamel plates are preserved on the wear surface, including two half-plates (the second and fourth from the front) which are together counted as one. At the posterior end, an estimated four additional plates are unworn. This gives a total of 14 preserved plates, within the range of *E. (P.) antiquus* M3s (Osborn, 1942; Guenther, 1977). Other features corresponding to *E. (P.) antiquus* are:

- the enamel plates in early to mid wear show the characteristic long central element, flanked by medial and lateral rings
- some of the plates show traces of a central, posteriorly-directed fold, although this is not strongly marked
- the low lamellar frequency and thick enamel are typical

Metrical characters are shown in Table 2.

Upper Dentition

Found in isolation from the skull, parts of three individual teeth are preserved.

M2A, GRE 50

This is the anterior part of a left upper molar (Text-fig. 9). Its large size indicates a second or third
Text-fig. 8 - Grevena elephant site: *Elephas (Palaeoloxodon) antiquus* Falconer & Cautley (1847); Complete view of the excavated area with the fossil findings, including the associated bovid tooth *in situ.*
Tab. 1 - Measurements of the Grevena elephant skull and mandible, in comparison with other skulls of *Elephas antiquus*.

Notes: The comparative skulls and mandibles are all mature adult males; data from Osborn (1942). The Steinheim tusk, marked with an asterisk, is not associated with the skull. The Pignatoro specimen is from Italy; probably Late Ice Age; the Steinheim specimens are from the late Middle Pleistocene (cf. Holsteinian interglacial) of Germany; the Godavari specimen is from India (*E. namadicus*, a probable synonym of *E. antiquus*).

<table>
<thead>
<tr>
<th>no.</th>
<th>molar</th>
<th>side</th>
<th>L</th>
<th>P</th>
<th>LF</th>
<th>W</th>
<th>H</th>
<th>e</th>
</tr>
</thead>
<tbody>
<tr>
<td>GRE151</td>
<td>M₂</td>
<td>right</td>
<td>242</td>
<td>6.0</td>
<td>82.7</td>
<td>-</td>
<td>2.3-2.9-3.3</td>
<td></td>
</tr>
<tr>
<td>GRE 50</td>
<td>M₂₂</td>
<td>left</td>
<td>-</td>
<td>5.6</td>
<td>89.0</td>
<td>149</td>
<td>2.4-2.6-2.9</td>
<td></td>
</tr>
<tr>
<td>GRE 51</td>
<td>M₂₂</td>
<td>left</td>
<td>-</td>
<td>x2</td>
<td>80.0</td>
<td>140</td>
<td>2.4-2.7-3.1</td>
<td></td>
</tr>
<tr>
<td>GRE 53</td>
<td>?</td>
<td>?</td>
<td>-</td>
<td>-</td>
<td>52.0</td>
<td>115</td>
<td>2.8-3.1-3.7</td>
<td></td>
</tr>
</tbody>
</table>

Tab. 2 - Measurements of elephant molars. Notes: Measurements (in mm) taken according to the method of Maglio (1973). L = preserved length of tooth, P = lamellar (plate) number, x = talon, - = lamellae lost by breakage, oo = lamellae lost by wear, LF = lamellar frequency: number of lamellae per 10 cm length of tooth, averaged between crown base and root, mediai and lateral. W = maximum molar width. In the mandibular molar, the maximum width is on the 7th plate, and includes cement. In no. GRE 50, the maximum width is on the 6th plate and is close to the tooth's maximum, except that some cement has been lost. In nos. GRE 51-52 and GRE 53, the widths are below the tooth's maximum. H = crown height, below the tooth's maximum in all specimens because of wear. e = enamel thickness, given as minimum, mode and maximum across the exposed surface.

molar. Six plates are preserved down to the crown base, but the roots are lost. The anteriormost plate represents the natural front of the tooth, and has its own connection to the root, i.e. there is no talon (small rootless first plate). Dimensions of the tooth are shown in Table 2. Several features of the upper tooth indicate its identity as straight-tusked elephant:

- the posterior preserved plate shows a 'dumbbell-shaped' occlusal pattern, i.e. a long central portion flanked by a small circular portion medially and laterally. Higher in the crown, these would have been 'pinched off' to form two separate rings;
- the enamel loops are strongly plicated, including one strong central plication and two pairs of strong plications medial and lateral to it;
- the enamel loops have a characteristic 'cigar-shaped' occlusal pattern;
- the lateral and medial faces of the enamel loops show clear longitudinal grooves when the tooth is viewed from the side;
- the thick enamel and low lamellar frequency (Table 2) are consistent with *E. (P) antiquus* but not with *Mammuthus* (except for the early Middle Pleistocene *M. trogontherii*).

**M₂₂**, GRE 51-52

This specimen comprises two isolated lamellae, which fit together, i.e. they were adjacent lamellae in a single tooth, but have become separated. The anterior of the two lamellae bears a small talon, with anterior (interstitial) wear from the preceding molar, indicating that this was the anteriormost lamella of the molar. The very oblique occlusal wear of the two lamellae confirms it as the anterior part of an upper molar. Its large size indicates either an M2 or M3. The tooth is from the left side, because the wear surface slopes down toward the lingual side.

Measurements of this specimen are shown in Table 2. Its enamel is too thick for *Mammuthus primigenius* or *M. trogontherii*, and the crown is too high for *M. meridionalis*. These measurements are consistent, however, with *Elephas (Palaeoloxodon) antiquus*, an identification confirmed by other features:

- the relatively narrow crown
- the small lateral ring on the occlusal surface of the posterior lamella
- strong grooves on the front and back of the lamellae, indicating that they would show clear plication in wear.
Figs. 1-3 - Excavation of Grevena elephant in 1995.
1) skull GRE 150, mandible GRE 151, epistropheus GRE 152 and rib GRE 153, in situ;
2, 3) the skull in situ.
The enamel of one of these lamellae was used for ESR dating (see Appendix).

GRE 53

This is a single, isolated, unworn lamella, whose shape suggests it is from the posterior region of a molar. It is narrow and has thick enamel (Table 2). It may come from the posterior part of the same molar as GRE 51-52.

Vertebral column, ribs and sternum

Vertebral column

Twelve vertebrae are preserved more-or-less complete: the axis (epistropheus), nine thoracics, one lumbar and one caudal. In addition, there is a fragment of a centrum from an unidentified vertebra. Two of the preserved vertebrae (first and second thoracics) were found together in life position, apparently cemented by sediment (Pl. 3, fig. 3). The vertebrae were allocated their positions in the column on the basis of trends in the morphology of centrum, transverse processes, articular facets and neural spines (Kroll, 1991). In some cases, however, the deduced position is approximate because many vertebrae are missing from the series. Identifications and measurements are given in Table 3.

The angle at which the dorsal spines are held relative to the vertebral body is an interesting feature which has been given taxonomic value. Andrews (1928) indicated that in the skeleton of *E. (P.) antiquus* from Upnor, near London, the thoracic and lumbar thoracic spines are held 'bolt upright', a condition unlike any other elephantid species. The angle between the dorsal spine and vertebral centrum has been measured on the Grevena vertebrae, and indicates values close to 180° ('bolt upright') for the posterior thoracic vertebrae nos. GRE 141, 118 and 126 (Table 3). On the other hand, Kroll (1991, p.65) gave measurements on four *E. (P.) antiquus* individuals from Germany which indicate that the thoracic and lumbar neural spines are markedly inclined toward the posterior. This feature therefore appears to show variation within the species.

Rib

Substantial parts of fourteen ribs have been recovered, six from the anterior part of the thorax (nos.
EXPLANATION OF PLATE 2

Figs. 1-3 - Mandible of Grevena elephant GRE 151
1) posterior view, 2) lateral view (in situ) 3) detail of the tooth, in situ.
APPENDICULAR
served
one
middle
plete:
Number
GRE
128
Measurements
respectively)
115
104
102,
100
101,
106,
112,
120,
121),
three
middle
region
(29,
134
110,
117,
123,
128).
The
arti-
head
pres-
five
anterior
and
mid-region
ribs,
with
maximum
diameters
ranging
from
89.8
- 91.0
mm.
Only
one
rib,
from
the
anterior
region,
is
preserved
complete;
its
contour
length
is
1200
mm.

Sternum
The
sternum
(GRE 24) is
preserved
complete,
all
three
parts
(presternum,
mesosternum
and
xiphister-
num)
being
fused
together.
Its
total
length
is
426
mm,
maximum
height
155
mm,
maximum
width
104
mm.

APPENDICULAR SKELETON

Scapula
Left
and
right
scapulae
(GRE
100
and
101,
respectively)
are
preserved
almost
complete
(PL
4,
figs.
2,
4).
The
dorsal
epiphysis
is
fused
to
the
blade.
Measurements
are
given
in
Table
4.

According
to
Trevisan
(1947)
and
Melentis
(1963),
the
spine
morphology
differs
between
Palaeoloxodon
and
Mammuthus.
However,
the
spine
is
too
crushed
in
both
Grevena
scapulae
to
observe
this
character.
The
overall
shape
of
the
scapula
also
appears
to
differ
between
these
genera,
that
of
Palaeoloxodon
being
less
deep
dorso-ventral
measurement)
for
its
length
(antero-posterior
measurement).
The
Grevena
scapulae
conform
to
this
'squat'
shape,
and
this
is
reflected
in
the
acute
angles
formed
between
the
dorsal
edge
and
the
anterior
and
posteri-
or
edges
(Table
4).

Humerus
A
fragment
of
the
lateral
part
of
the
distal
epiph-
ysis
of
the
left
humerus
is
preserved
(no.
75).
The
antero-posterior
diameter
of
the
condyle
is
184
mm.
This
specimen
articulates
well
with
the
left
ulna
(no.
90)
when
the
two
are
brought
together.

Ulnea
Part
of
the
lateral
facet
of
the
proximal
articu-
lar
surface
of
the
left
ulna
(no.
90)
is
preserved.
Another
fragment
(no.
80)
is
a
portion
of
the
distal
epiphysis
of
the
right
ulna.
The
full
antero-posterior
diameter
of
the
distal
articulation
is
preserved,
and
measures
134
mm.
The
fusion
state
of
the
epiphysis
is
unclear.

EXPLANATION
OF
PLATE
3
Figs.
1-3
Thoracic
vertebrae
of
Grevena
elephant.
1) (from
bottom
to
top
GRE
126
and
118:
1a)
posterior
view,
1b)
lateral
view.
2) GRE
125:
2a)
posterior
view,
2b)
lateral
view.
3) First
and
second
thoracic
vertebrae
GRE
115,
116,
in
situ.
Tab. 4 - Measurements of scapulae (mm).

<table>
<thead>
<tr>
<th>Number</th>
<th>Side</th>
<th>Length (parallel to spine)</th>
<th>Width (perpendicular to spine)</th>
<th>Width (parallel to dorsal edge)</th>
<th>Neck width (minimum)</th>
<th>Glenoid diameter (antero-posterior)</th>
<th>Glenoid diameter (medio-lateral)</th>
<th>Distal diameter (antero-posterior)</th>
<th>Angle between posterior and dorsal edges</th>
<th>Angle between anterior and dorsal edges</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>R</td>
<td>1010</td>
<td>885</td>
<td>1035</td>
<td>330</td>
<td>280</td>
<td>164</td>
<td>373</td>
<td>72°</td>
<td>50°</td>
</tr>
<tr>
<td>101</td>
<td>L</td>
<td>1040</td>
<td>-</td>
<td>1000</td>
<td>323</td>
<td>-261</td>
<td>-170</td>
<td>-</td>
<td>66°</td>
<td>50°</td>
</tr>
</tbody>
</table>

Radius

A fragment of the distal epiphysis of the right radius (no. 73A) is preserved. It had clearly not yet fused to the diaphysis.

Forefoot

The majority of bones of the right forefoot have been recovered. These are the lunatum (no. 61), cuneiform (pyriform) (no. 32), pisiform (no. 5), magnum (no. 30), unciform (no. 60), trapezium (no. 7), metacarpal I (no. 13), metacarpal II (no. 15), metacarpal III (no. 2), metacarpal IV (no. 3), metacarpal V (no. 4), and proximal phalanx III (no. 1). Thus, of the carpal and metacarpal bones, all except the scaphoid (navicular) and trapezoid have been recovered. Other phalanges (see below) probably belong to this foot; but their position could not be definitely identified. Metacarpals II-V, and proximal phalanx II, were found in anatomical order (Pl. 4, fig. 1).

The left forefoot is less well represented, with only the scaphoid (no. 81), magnum (no. 94) and unciform (nos. 76-96) preserved.

Measurements of these bones are given in Tables 5 and 6.

Patella

The left patella (no. 6) has been recovered. Its maximum dimensions are 196.5 mm (dorso-ventral), 145.4 mm (medio-lateral) and 120.5 mm (antero-posterior).

Fibula

The complete right fibula (no. 127) is preserved (Pl. 4, fig. 3). Its measurements (in mm) are: length 840, proximal depth (antero-posterior) 89.8, proximal width (medio-lateral) 72.4, distal depth 158.0, distal width 96.0.

Tibia

Specimen no. 85 is fragment of the anterior face of the left tibia, including the cnemial crest. Specimen no. 82 is a fragment of the posterior wall of a tibia, side indeterminate.

Hindfoot

The proximal and lateral parts of the right hindfoot have been recovered. The elements preserved are the calcaneum (no. 23), astragalus (no. 40), navicular (no. 38), cuboid (no. 119), metatarsal IV (no. 20) and metatarsal V (no. 41). The astragalus measurements (in mm) are as follows: maximum medio-lateral diameter (width) 179.3, maximum antero-posterior diameter (depth) 169.8, medio-lateral diameter (width) of proximal facet 141.4, dorso-ventral diameter (height) of navicular facet 92.3. The calcaneum measurements are: length 289.0, medio-lateral diameter (width) 195.2, width of tuber calcanei 190.0, length, excluding distal facets 276.0. Measurements of the more distal bones of the hind foot are given in Tables 5 and 6. Some phalanges (see below) may belong to this foot, but their position could not be ascertained with certainty.

Phalanges

In addition to the right first phalanx III of the forefoot (no. 1) mentioned above, eleven further phalanges have been recovered, but their precise position (left or right, fore or hind) is not known. They comprise six further first phalanges, (nos. 12, 32, 36a, 56, 57 and 58), three second phalanges (nos. 10, 21 and

EXPLANATION OF PLATE 4

Fig. 1 - Grevena excavation of 1992, showing associated foot bones and other remains.
Fig. 2 - Grevena excavation of 1994
Fig. 3 - Fibula GRE 127 in situ.
Fig. 4 - Right scapula GRE 100, in situ on the silty clays, with stratigraphic column of the Grevena Formation in the back ground.
<table>
<thead>
<tr>
<th>Number</th>
<th>Element</th>
<th>Medio-lateral diameter of anterior face</th>
<th>Antero-posterior diameter (perpendicular to anterior face)</th>
<th>Dorso-ventral diameter of anterior face</th>
<th>Maximum dorso-ventral diameter of bone</th>
</tr>
</thead>
<tbody>
<tr>
<td>81</td>
<td>L. scaphoid</td>
<td>64.5</td>
<td>132.4</td>
<td>94.0</td>
<td>160.6</td>
</tr>
<tr>
<td>61</td>
<td>R. lunatum</td>
<td>160.0</td>
<td>&gt;157</td>
<td>83.0 (excluding lateral process)</td>
<td>183.0</td>
</tr>
<tr>
<td>32</td>
<td>R. cuneiform</td>
<td>241.8</td>
<td>157.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>R. pisiform</td>
<td>90.5 (prox. end)</td>
<td>70.0 (prox. end)</td>
<td>133.8</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>R. magnum</td>
<td>121.5</td>
<td>165.0</td>
<td>130.3</td>
<td></td>
</tr>
<tr>
<td>94</td>
<td>L. magnum</td>
<td>-</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>60</td>
<td>R. unciform</td>
<td>169.5</td>
<td>155.3</td>
<td>127.2</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>R. trapezium</td>
<td>63.0</td>
<td>103.0</td>
<td>98.0</td>
<td></td>
</tr>
<tr>
<td>38</td>
<td>R. navicular</td>
<td>167.3</td>
<td>124.2</td>
<td>49.5</td>
<td></td>
</tr>
<tr>
<td>119</td>
<td>R. cuboid</td>
<td>133.9</td>
<td>131.9</td>
<td>63.3</td>
<td></td>
</tr>
</tbody>
</table>

Tab. 5 - Measurements of carpal and tarsal bones.  
Notes: The diameters of carpal and tarsal bones (with the exception of the pisiform) are measured on the flat anterior face of the bone. Depths are taken at right angles to this face.

<table>
<thead>
<tr>
<th>number</th>
<th>bone</th>
<th>length</th>
<th>proximal w</th>
<th>proximal d</th>
<th>distal w</th>
<th>distal d</th>
<th>shaft w</th>
<th>shaft d</th>
</tr>
</thead>
<tbody>
<tr>
<td>13</td>
<td>R. metacarpal I</td>
<td>160.5</td>
<td>-</td>
<td>107.0</td>
<td>82.9</td>
<td>83.3</td>
<td>50.7</td>
<td>69.5</td>
</tr>
<tr>
<td>15</td>
<td>R. metacarpal II</td>
<td>216.8</td>
<td>93.1</td>
<td>128.2</td>
<td>111.3</td>
<td>98.7</td>
<td>76.3</td>
<td>68.0</td>
</tr>
<tr>
<td>2</td>
<td>R. metacarpal III</td>
<td>254.4</td>
<td>104.8</td>
<td>126.5</td>
<td>118.8</td>
<td>108.4</td>
<td>86.3</td>
<td>61.6</td>
</tr>
<tr>
<td>3</td>
<td>R. metacarpal IV</td>
<td>223.7</td>
<td>112.8</td>
<td>110.4</td>
<td>120.5</td>
<td>105.7</td>
<td>94.6</td>
<td>61.9</td>
</tr>
<tr>
<td>4</td>
<td>R. metacarpal V</td>
<td>205.2</td>
<td>115.6</td>
<td>98.8</td>
<td>115.8</td>
<td>109.5</td>
<td>85.3</td>
<td>69.2</td>
</tr>
<tr>
<td>20</td>
<td>R. metatarsal IV</td>
<td>169.4</td>
<td>96.6</td>
<td>87.6</td>
<td>98.7</td>
<td>83.6</td>
<td>77.7</td>
<td>48.5</td>
</tr>
<tr>
<td>41</td>
<td>R. metatarsal V</td>
<td>112.5</td>
<td>101.2</td>
<td>93.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>R. ant. phalanx I</td>
<td>114.9</td>
<td>84.7</td>
<td>78.3</td>
<td>83.7</td>
<td>52.3</td>
<td>68.4</td>
<td></td>
</tr>
<tr>
<td>36,57</td>
<td>R. +I. phalanx I</td>
<td>115.0</td>
<td>101.0</td>
<td>83.0</td>
<td>86.0</td>
<td>52.7</td>
<td>78.5</td>
<td>51.3</td>
</tr>
<tr>
<td>56</td>
<td>Phalanx I</td>
<td>112.5</td>
<td>84.1</td>
<td>77.0</td>
<td>71.0</td>
<td>56.4</td>
<td>69.0</td>
<td>47.0</td>
</tr>
<tr>
<td>12</td>
<td>Phalanx I</td>
<td>117.0</td>
<td>82.5</td>
<td>77.7</td>
<td>66.5</td>
<td>60.5</td>
<td>65.8</td>
<td>47.0</td>
</tr>
<tr>
<td>32a</td>
<td>Phalanx I</td>
<td>100.0</td>
<td>-</td>
<td>62.0</td>
<td>(69.0)</td>
<td>42.4</td>
<td>(69.5)</td>
<td>41.8</td>
</tr>
<tr>
<td>58</td>
<td>Phalanx I</td>
<td>77.2</td>
<td>66.0</td>
<td>65.5</td>
<td>61.5</td>
<td>44.3</td>
<td>57.8</td>
<td>41.8</td>
</tr>
<tr>
<td>10,59</td>
<td>R. +I. Phalanx II</td>
<td>64.3</td>
<td>71.0</td>
<td>47.5</td>
<td>59.0</td>
<td>31.2</td>
<td>62.5</td>
<td>31.5</td>
</tr>
<tr>
<td>21</td>
<td>Phalanx II</td>
<td>58.8</td>
<td>68.5</td>
<td>47.5</td>
<td>59.7</td>
<td>30.6</td>
<td>63.0</td>
<td>31.6</td>
</tr>
</tbody>
</table>

Tab. 6 - Measurements of metapodials and phalanx I.  
Notes: Length measured parallel to the long axis of the bone. Metatarsal V is a strongly twisted bone, making measurements difficult to define. 'Proximal width' is the maximum width for the whole bone, taken parallel to the distal articulation. 'Proximal depth' is a maximum depth for the whole bone.

59), and two fragmentary third phalanges (nos. 8 and 18). The first and second phalanges are asymmetrical and so pertain to digits other than III. The measurements of all these elements are given in Table 6.

**Sesamoids**

Fifteen sesamoid bones have been recovered, of varying sizes. These are numbers 9, 11, 14, 16, 17, 19, 62-69 and 97. The largest (no. 14) has a maximum diameter of 88.2 mm.

**AGE, SIZE AND GENDER OF THE ELEPHANT**

**AGE**

Evidence on the ontogenetic age of the skeleton is provided by the stage of dental progression and wear, and the state of fusion of the limb bones.

The Grevena mandible includes a single tooth which has been interpreted as the last (third) molar, in middle wear, with a few plates lost at the front, a few unworn behind, and the majority in wear. This wear stage, in both living Asian and African elephants, indicates a mature adult in its 40s (Laws, 1966; Roth & Shoshani, 1988; Jachmann, 1988; Haynes, 1991). Note that this does not necessarily indicate true years, but 'dental years' or 'Equivalent Years' (Laws, 1966). Because [Palaeoloxodon], on the basis of its larger body size, probably had a longer total lifespan than living elephants, the true age at a given state of dental progression may have been somewhat older (Lister, 1994).

In elephants, the different limb bone epiphyses fuse in a systematic fashion with age, a similar pattern occurring in all species studied (African elephant:

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*E. TSOUKALA, A. LISTER*
Haynes, 1991; Asian elephant: Roth, 1984; woolly mammoth: Lister, 1994). The Grevena skeleton shows the fusion state of two major epiphyses: the dorsal border of the scapula, which is fused, and the distal radius epiphysis, which is unfused. In living elephant males, these bones are among the last to fuse, the scapula fusing in the animal's late 30s, the distal radius and ulna in its late 40s. In females the figures are somewhat younger. It can be deduced that the Grevena elephant was, in terms of the modern elephant lifespan, in its 40s. As with the dentally-based estimate, these are not necessarily true years, but 'Equivalent Years' (Laws, 1966). It is striking, however, that the dental progression and epiphysis fusion of the Grevena skeleton correspond precisely, indicating a mature, fully-grown adult entering the last third of the species' typical lifespan.

**SIZE AND GENDER**

The size of selected elements of the Grevena skeleton is compared to known male and female *E. (P) antiquus* in Tables 1 and 7. Comparative data is taken from Osborn (1942), Aguirre (1969) and Kroll (1991). Although the comparative samples are small, the difference in size between males and females in postcranial elements is clear and non-overlapping, and the Grevena animal falls very clearly into the male category, probably in the upper half of the range. Measurements of female skulls are not available, but the Grevena skull is in the upper part of the size range of male skulls tabulated by Osborn (1942) (Table 1). Lister and Agenbroad (1994) and Lister (1996b) showed how the proportions of the pelvic girdle can be used to determine gender in elephants, but this element has not been recovered at Grevena.

According to Kroll (1991), the reconstructed height at the shoulder of male *E. (P) antiquus* ranged from 3.80–4.30 metres (n=6), so the Grevena elephant, in the upper half of the male size range, was probably about 4.0–4.2 metres in shoulder height.

**ASSOCIATION AND COMPLETENESS OF SKELETON**

It is very likely that almost all the remains found at Grevena belong to a single individual of *Elephas (Palaeoloxodon) antiquus*. They were found in a small area, no elements are duplicated, and many of them articulate well. In addition, their size and ontogenetic age are all conformable (Text-fig. 10).

The only possible exceptions to this are the isolated parts of upper molars. First, the isolated lamellae, GRE 51-52, represent the anterior part of a left upper molar, thereby duplicating the more complete left upper molar GRE 50. Specimens GRE 50 and 51-52 cannot be sequential teeth of the same individual because both show the anterior part of the tooth preserved and in wear. Such a situation never occurs in a living elephant. The more complete tooth, GRE 50, corresponds in its appearance and preservation to the rest of the skeleton, whereas the isolated plates GRE 51-52 and 53 have a different preservation and seemingly came from a different individual.

However, both of the upper molar fragments GRE 50 and 51-52 are at a much earlier wear stage than the lower molar preserved in the mandible. The latter, thought to be an M3, is worn right down to the base anteriorly, with several plates probably lost through wear (see above). The upper molar pieces, by contrast, retain a substantial height of crown (at least 3 cm even at the anterior end), and no plates are lost through wear. Even assuming that these teeth are M3s rather than M2s (see above), they are at a significantly earlier wear stage than the mandibular tooth. Although upper and lower teeth of an individual can be at somewhat differing wear stages, the degree of difference seen among the Grevena material suggests that the three upper molar pieces represent at least two individuals additional to that represented by the mandible and the rest of the skeleton.

The position of the two scapulae *in situ* (Text-fig. 8) suggests that the elephant was lying on its right

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**Tab. 7 - Size of selected elements of the Grevena postcranial skeleton in comparison with other *Elephas (Palaeoloxodon) antiquus* skeletons.**

Notes: comparative measurements of teeth taken from Aguirre (1969); of postcranial bones, from Kroll (1991). Measurements quoted to nearest mm. The upper M3 from Grevena may not be associated with the skeleton (see text).
side: the right scapula was medial side up, the left scapula lateral side up. The right front foot is preserved almost complete, as are the fibula and parts of the right back foot, all with excellent bone preservation. By contrast, little of the left front foot, and none of the left back foot, have been recovered, and the bones are damaged. These data suggest that the left side of the animal, lying slightly higher, was more subject to bone loss and erosion than the right side. The skull and mandible both came to lie ventral side up, but the mandible was detached from the skull and lies nearby, rotated 180 degrees relative to its anatomical position on the skull.

ASSOCIATED REMAINS

Family Bovidae Gray 1821
Sub-family Bovinae Gill 1821
Genus Bos L. 1758
Bos primigenius Bojanus, 1827

MATERIAL

Right upper molar M₁/₂, GRE 131; right lower molar M₂, GRE 149.

DESCRIPTION

Only two molars of a large bovid were found in association with the elephant skeleton. The upper one (M₁/₂ GRE 131) was found close to the rib GRE 129 (Text-fig. 8) and the lower one (M₂, GRE 149) was recovered in sieving, from sediment taken close to the scapula GRE 100. The upper molar is in middle wear, with the palatinal part of the hypocone and the endostyle missing. Its dimensions suggest a second molar. The slightly to little-worn lower molar is very well preserved. Between the lobes, with intensely wrinkled enamel, the ectostyloid is well developed, up to the two thirds of the tooth height. It is a second molar, shown both by the morphology and by the dimensions of the tooth. According to Slott-Moller (1993/4), separation between the genera Bos and Bison is possible using the ectostyloid diameter of the lower molars, measured in the middle of their height: in Bison the ectostyloid is said to be notably larger on average than in Bos. On this criterion, the ectostyloid in the Grevena specimen is clearly narrow, suggesting Bos. However, caution should attach to this determination as the character appears to be quite variable within species (P. Mazza, pers. comm.). The breadth/length index (Table 8) and the dimensions show the tooth to be relatively robust.

DISCUSSION

Straight-tusked elephant has previously been recorded at only 11 localities in Greece, among a total of 23 localities with Pleistocene elephantids, excluding island endemics (Text-fig. 11 and Table 9). There is undoubtedly more material in museum collections, and some specimens of E. (P) antiquus have been published under other names, for example the maxilla from Perdikas figured by Poulianos & Poulianos (1980) as 'Archidiskodon meridionalis'. In the case of the latter specimen, the loxodont form of the lamellae, crenulated enamel, strong median folds, and narrow crown leave no doubt of the identity of this specimen as E. (P) antiquus. Evidence to date indicates that E. (P) antiquus arose from the African E. recki (Maglio, 1973), and first entered Europe in the early Middle Pleistocene (Lister, 1996c). A Pliocene age for the Perdikas specimen, suggested by Poulianos &
Poulianos (1980), therefore seems unlikely. In any case, other fossils found in the Perdikas Formation indicate a Late Pleistocene age (Pavlides, 1985).

There is also some confusion surrounding the identity of the island populations. Dwarfed elephants, referred to endemic species but clearly derived from *E. (P) antiquus*, are found on several Greek islands (Symeonidis & Theodorou, 1982; Dermitzakis et al., 1982; Tsoukala, 1992), such as Tilos (Theodorou, 1983). Various researchers have suggested that the insular proboscideans from Crete include some full-sized elephants, which perhaps represent founder populations of *E. (P) antiquus*. However, Theodorou (1986) does not accept these determinations.

Elephas (*Paleoloxodon*) *antiquus* has been divided by some authors into subspecies, of which the most commonly cited are the supposed 'German' subspecies *E. (Paleoloxodon) antiquus germanicus* Stefanescu, 1924 and the supposed 'Italian' subspecies *E. (P) antiquus italicus* Osborn, 1931. According to Trevisan (1948) and Adam (1953), the *italicus* form is characterised by a larger size and greater number of molar lamellae than the *germanicus* form. However, the validity of these differences has never been demonstrated statistically. Material from Greece has at times been referred to both 'subspecies' (Melentis, 1961, 1963, 1965; Dermitzakis et al., 1982). The Grevena skeleton cannot alone contribute to this debate, but will form part of a full review cur-

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**Tab. 8 - Dimensions of teeth of *cf. Bos primigenius*, found in association with the elephant remains at Grevena.**

<table>
<thead>
<tr>
<th>LOCALITY</th>
<th>RESEARCHER</th>
<th>TAXON</th>
</tr>
</thead>
<tbody>
<tr>
<td>Drama</td>
<td>Koufos 1981</td>
<td>Manumutus <em>cf. primigenius</em></td>
</tr>
<tr>
<td>Philippoi</td>
<td>Dermitzakis et al. 1982</td>
<td><em>M. trogontherii, A. meridionalis</em></td>
</tr>
<tr>
<td>Serres</td>
<td>Dermitzakis et al. 1982</td>
<td>Archidiskodon meridionalis</td>
</tr>
<tr>
<td>Epanomi</td>
<td>Dermitzakis et al. 1982</td>
<td><em>Elephas</em> (<em>Paleoloxodon</em>) <em>antiquus</em></td>
</tr>
<tr>
<td>Telphos</td>
<td>Dermitzakis et al. 1982</td>
<td><em>Elephas</em> (<em>Paleoloxodon</em>) <em>antiquus</em></td>
</tr>
<tr>
<td>Alatini</td>
<td>Dermitzakis et al. 1982</td>
<td><em>Elephas</em> (<em>Paleoloxodon</em>) <em>antiquus</em></td>
</tr>
<tr>
<td>Vathykalos (Axios)</td>
<td>Dermitzakis et al. 1982</td>
<td><em>Elephas</em> (<em>Paleoloxodon</em>) <em>antiquus</em></td>
</tr>
<tr>
<td>Larisa</td>
<td>Boessneck 1965</td>
<td>A. meridionalis, <em>Manumutus cf. primigenius</em></td>
</tr>
<tr>
<td>Penios river</td>
<td>Dermitzakis et al. 1982</td>
<td>Archidiskodon meridionalis archaicus</td>
</tr>
<tr>
<td>Ioannina</td>
<td>Melentis 1960</td>
<td>Archidiskodon meridionalis archaicus</td>
</tr>
<tr>
<td>Neapolis (Polyalakos, Libakos, Kapetanios, Aliakmon river)</td>
<td>Mitzopoulos 1967</td>
<td>A. meridionalis archaicus</td>
</tr>
<tr>
<td>Prolernais basin (Sotir, Amynteon, etc)</td>
<td>Mitzopoulos 1967, Steenma 1988</td>
<td>(Elephas (<em>Paleoloxodon</em>) <em>antiquus</em>)</td>
</tr>
<tr>
<td>Perdikas</td>
<td>Poulianos &amp; Poulianos 1980</td>
<td><em>E. (P) antiquus, A. meridionalis</em></td>
</tr>
<tr>
<td>Aliakmon (Toryli)</td>
<td>Poulianos &amp; Poulianos 1980</td>
<td><em>Elephas</em> (<em>Paleoloxodon</em>) <em>antiquus</em></td>
</tr>
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<td>Grevena</td>
<td>Melentis 1966</td>
<td>Archidiskodon meridionalis</td>
</tr>
<tr>
<td>Limni</td>
<td>PRESENT STUDY</td>
<td>Archidiskodon meridionalis</td>
</tr>
<tr>
<td>Aidipos</td>
<td>Dermitzakis et al. 1982</td>
<td>Archidiskodon meridionalis</td>
</tr>
<tr>
<td>Imvros island</td>
<td>Dermitzakis et al. 1982</td>
<td>Archidiskodon meridionalis</td>
</tr>
<tr>
<td>Kos island</td>
<td>Dermitzakis et al. 1982</td>
<td>Archidiskodon meridionalis</td>
</tr>
<tr>
<td>Crete island</td>
<td>Dermitzakis et al. 1982</td>
<td>Archidiskodon meridionalis</td>
</tr>
<tr>
<td>Kythera island</td>
<td>Symposiumis &amp; Theodorou 1985/86</td>
<td>Archidiskodon meridionalis</td>
</tr>
<tr>
<td>Megalopolis</td>
<td>Sickenberg 1976</td>
<td><em>E. (P) a. (italicus germanicus)</em></td>
</tr>
</tbody>
</table>

Tab. 9 - Records of fossil elephants in Greece, excluding endemic island species. Taxonomic assignments are those of the original authors. The specimen from Perdikas (no. 13) is here reassigned to *Elephas* (*Paleoloxodon*) *antiquus*. 

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**M*<sup>1</sup> GREGRE*<sup>131</sup> | **M*<sup>2</sup> GREGRE*<sup>149</sup> |
<table>
<thead>
<tr>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1. L (length)</td>
<td>31.4</td>
</tr>
<tr>
<td>2. B (breadth)</td>
<td>27.0</td>
</tr>
<tr>
<td>3. L:B:L (%)</td>
<td>86</td>
</tr>
<tr>
<td>4. D ectostyld (diameter in the middle)</td>
<td>34.3 (38.8 max. occlusal)</td>
</tr>
<tr>
<td>5. H ectostyld</td>
<td>2.6</td>
</tr>
<tr>
<td>6. H (height)</td>
<td>43.2</td>
</tr>
<tr>
<td>7. H (height)</td>
<td>68.0</td>
</tr>
</tbody>
</table>

Tab. 8 - Dimensions of teeth of *cf. Bos primigenius*, found in association with the elephant remains at Grevena.
of the localities of continental Pleistocene elephants. The localities are listed in Tab. 9.

Text-fig. 11 - Map of Greece with

Currently being undertaken (P. Davies, UCL). Along with the Perdikas specimen, it is one of the two most complete skeletons of straight-tusked elephant known from Greece, but the Perdikas specimen has not been described in detail. The Grevena skeleton, a large male, adds significantly to the limited knowledge of the range of variation of this species as a whole.

Dating of the isolated lamella GRE 51, by Electron-Spin-Resonance (see Appendix), indicates an age of 160-170 kyr for this specimen. Although these lamellae appear to represent a different individual from the main Grevena skeleton, it is likely that all these remains, found in one horizon and with no evidence of re-working (all the dental remains are very fresh-looking), are of similar age. In any case, the dated lamellae indicate the presence of Elephas (Palaeoloxodon) antiquus in Greece during Oxygen Isotope Stage 6 (OIS 6). In northern and central Europe, E. (P.) antiquus is generally regarded as an interglacial indicator, being present during temperate, wooded episodes corresponding to odd-numbered OIS stages (Stuart, 1982). During intervening cold episodes, the species is generally absent from these regions. Occasional exceptions, presumably correponding to milder intervals (interstadials) are recorded, for example at the Snitterfield site in the English Midlands, in Middle Pleistocene cold-stage gravels pertaining to either OIS 12 or 10 (Lister et al., 1990; Rose, 1987). However, for the majority of these long, cold episodes, the range of E. (P.) antiquus is presumed to have contracted to the south. The dating of the Grevena elephant remains to OIS 6 corroborates this suggestion, indicating northern Greece as part of the glacial refugium of the species. A similar situation pertains to the bovid remains, referred to Bos, from the same horizon. This taxon, too, is an interglacial indicator in northern and central Europe, largely absent during 'cold stages' (Stuart, 1982). As for the straight-tusked elephant, Mediterranean Europe presumably acted as a refuge during glacial episodes.

ACKNOWLEDGEMENTS

Our sincerest thanks are due to all who contributed to this research over several years, especially the leaders of the Prefecture and the Mayors of Grevena town. Many thanks especially to Mr. Dimitrios Douros who supported this effort through the Prefecture of Grevena. We are also grateful to those who helped with the excavations: E. Chatzieletheriou, V. Makridis (Kilkis),
E. Baltakis (Aridea), I. Ioakimidis, and the geologists N. Kourambas, G. Douros, E. Chouliara, M. Moutsiki, G. Nastos, K.C. Douros, I. Sourou, A. Vassiliadou and K. Chagioupolou. Finally, many thanks to our colleagues, Associate Professor Dr. S. Pavlidis for discussion on the geological context, and Dr. E. Bassiakos for the ESR dating. B. Mazza and P. Davies kindly commented on the draft manuscript.

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**APPENDIX**

**ESR DATING OF ELEPHANT TOOTH ENAMEL**

by Y. BASSIAKOS, Laboratory of Archaeometry, N.C.S.R. "Demokritos", Athens.

Enamel from an isolated molar lamella (specimen GRE 51) was used for ESR-dating studies. This material, with its thick enamel protected by cementum and dentine, has been shown to be particularly suitable for the ESR technique (Grön, 1989).

By mechanical separation, the outer layers of enamel (1 mm on each side) were removed, and the remaining sample was used for ESR (EPR) spectroscopy. Three successive slices of the lamella were taken for dating. Fission-track studies for the exact determination of U-content and microdistribution were carried out in vertical, horizontal and plan sections of the molar. The parameters for ESR-spectroscopy are given in a previous paper (Bassiakos & Tsoukala, 1996, table 5).

The external dose-rate was measured in situ by means of a calibrated portable scintillator (GIS-4, SCINTREX, NaI (Tl) crystal). The U and Th content of the surrounding soil was determined by means of a spectroscopy, while AA analysis gave the K-concentra-

<table>
<thead>
<tr>
<th>DESCRIPTION</th>
<th>GRE 51a</th>
<th>GRE 51b</th>
<th>GRE 51c</th>
</tr>
</thead>
<tbody>
<tr>
<td>AD (archaeological (geological) dose</td>
<td>318.06 Gy</td>
<td>330.12 Gy</td>
<td>324.20 Gy</td>
</tr>
<tr>
<td>DR (external dose rate)</td>
<td>950 μGy</td>
<td>960 μGy</td>
<td>960 μGy</td>
</tr>
<tr>
<td>U (content in enamel)</td>
<td>957 ppm</td>
<td>960 ppm</td>
<td>960 ppm</td>
</tr>
<tr>
<td>U (content in dentine)</td>
<td>33.10 ppm</td>
<td>33.10 ppm</td>
<td>33.10 ppm</td>
</tr>
<tr>
<td>U (content in sediment)</td>
<td>2.95 ppm</td>
<td>2.95 ppm</td>
<td>2.95 ppm</td>
</tr>
<tr>
<td>Th (content in sediment)</td>
<td>9.8 ppm</td>
<td>10.1 ppm</td>
<td>10.0 ppm</td>
</tr>
<tr>
<td>K (content in sediment)</td>
<td>1.5%</td>
<td>1.8%</td>
<td>1.4%</td>
</tr>
<tr>
<td>K factor of enamel</td>
<td>0.15</td>
<td>0.15</td>
<td>0.15</td>
</tr>
<tr>
<td>Water content of dentine</td>
<td>17%</td>
<td>17%</td>
<td>17%</td>
</tr>
<tr>
<td>Water content of sediment</td>
<td>20%</td>
<td>20%</td>
<td>20%</td>
</tr>
<tr>
<td>Res.-loss of dentine</td>
<td>20%</td>
<td>20%</td>
<td>20%</td>
</tr>
<tr>
<td>Res.-loss of sediment</td>
<td>25%</td>
<td>25%</td>
<td>25%</td>
</tr>
<tr>
<td>Initial ratio U-234/U-238</td>
<td>1.3±0.1</td>
<td>1.3±0.1</td>
<td>1.3±0.1</td>
</tr>
<tr>
<td>T**: Age by Complex program</td>
<td>166,000±23,000</td>
<td>α</td>
<td>170,000±25,000</td>
</tr>
<tr>
<td>with Linear U-uptake</td>
<td></td>
<td>α</td>
<td></td>
</tr>
</tbody>
</table>

Appendix: Tab. 1 - Various values (measured, assumed, or taken from the literature) of necessary parameters for the ESR dating.
tion of the soil. For the AD estimation the LU model for U-uptake was assumed, based on equations given by Grün (1989). The assessment of Rn-loss for dentine and sediment was based on previous microscopic observation for crack density and porosity of dentine, and for grain size/compactness of soil.

The results of the ESR-dating of the material are summarised in Appendix Table I.

REFERENCES


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