A morphological study of the tooth roots of the Sima del Elefante mandible (Atapuerca, Spain): a new classification of the teeth—biological and methodological considerations

Leyre Prado-Simón1,2*, María Martinón-Torres1, Pilar Baca2, Aida Gómez-Robles1,3, María Lapresa1, Eudald Carbonell1, José María Bermúdez de Castro1

1Dental Anthropology Group, National Research Centre for Human Evolution, Burgos 09002, Spain
2Stomatology Department, Dentistry Faculty, University of Granada E-18071, Spain
3Konrad Lorenz Institute for Evolution and Cognition Research, Altenberg A-3422, Austria
4Institut Català de Paleoecologia Humana i Evolució Social, Àrea de Prehistoria, Universitat Rovira i Virgili, Tarragona ES-43003, Spain

Received 24 January 2011; accepted 28 September 2011

Abstract The recent application of microtomographic techniques to dental morphological studies has revealed an untapped source of biological information about extinct and extant human populations. In particular, this methodology has helped to characterize internal dental structures (enamel–dentine junction, pulp chamber, and radicular canals), maximizing the amount of information that can be extracted from a given specimen. In this study, we present a three-dimensional evaluation of the dental roots of the Sima del Elefante mandible, ATE9-1 (Atapuerca, Spain) by visual inspection, and by tomographic and microtomographic techniques. With 1.3 Myrs of age, this fossil represents the earliest hominin remains in Europe, and one of the very few human fossils for this period and region. Through this case study we aim to present a protocol for the description of the internal dental spaces, exemplify how the application of microtomographic techniques can significantly increase the amount of relevant and informative morphological features (even in the case of fragmentary/heavily worn teeth or teeth with hypercementosis), and explore some biological considerations about external and internal root morphology. There is neither a general nor straightforward correspondence between the external root morphology and the root canals. In cases where a high degree of hypercementosis is present, the external root anatomy can be highly confusing. Indeed the assessment of the internal root anatomy of ATE9-1 teeth has led us to the reclassification of the LC and the LP3 with respect to previous publications. The results of this study suggest that internal root anatomy could be used as a complementary source of biological information.

Key words: Microtomography, root canals, dental pulp, Sima del Elefante

Introduction

Teeth constitute the majority of fossil hominid collections (e.g. Hillson, 1996). The external and internal morphological details, development and tissue proportions of hominoid and hominin teeth have been extensively studied. The study of tooth crown and root morphology (e.g. Abbot, 1984; Wood et al., 1988; Bailey, 2002; Gómez-Robles et al., 2007; Martinón-Torres et al., 2008; Kupecz and Dean, 2008; Kupecz and Hublin, 2010), teeth development (e.g. Ramirez Rozzi and Bermúdez de Castro, 2004; Bayle et al., 2009a, b, 2010), enamel thickness (e.g. Kay, 1981; Martin, 1985; Kono et al., 2002; Olejniczak et al., 2008), enamel–dentine junction shape (e.g. Korenhof, 1961; Skinner et al., 2008; Bailey et al., 2011), tooth microwear and microtexture (e.g. Scott et al., 2005), and the incremental development of these tissues (e.g. Dean et al., 2001; Lacruz and Bromage, 2006; Smith et al., 2007; Guatelli-Steinberg and Reid, 2008; Smith et al., 2010) have increased our understanding of the fossil hominin species’ diet, life history, and phylogenetic relationships.

The space inside the dentine of the tooth where the pulp (the vascular nervous system of the tooth) is housed is called the pulp cavity. Dentine and pulp form a structural and functional unit, the dentino-pulp complex (Gómez and Campos, 2004). When dentine grows, the pulp cavity gets smaller. The deposition of the primary dentine starts with dentino-genesis and ends when the root apex is closed. Primary dentine constitutes the major part of the whole dentine of the teeth (Gómez and Campos, 2004). The formation of the secondary dentine starts when the root apex closes. Its production, at a lower rate than primary dentine, is continuous during the complete life of the tooth. With age, the secondary dentine deposition produces a reduction of the pulp cavity (Prapanpoch and Cottone, 1992; Solheim, 1993). The
The pulp cavity is divided into two portions: the pulp chamber, which is located in the anatomical crown of the tooth and the pulp or root canal or canals which are found in the anatomical root. The vascular-nervous system enters the root canal system via apical foramina at the root tips, and is distributed throughout the pulp cavity, forming multiple paths that lead to the pulp chamber that have complicated divisions between them. These complicated paths are formed by the entrapment of periodontal vessels in Hertwig’s epithelial root sheath during calcification (Cutright and Bhaskar, 1969). After crown formation, epithelial cells continue their proliferation to the tooth apex and produce a tubular sheath named Hertwig’s epithelial sheath (HERS), from which horizontal processes develop. The shape and folding of this sheath determines root structure (single or multi-rooted) (Kovacs, 1971). Deviations in the invagination process produce variations in root morphologies (Wright, 2007).

It is difficult to visualize and quantify the pulp cavity because it is an internal space rather than a directly observable surface. Although some aspects of the pulp cavity’s morphology (e.g. taurodontism) have been often discussed (e.g. Trinkaus, 1978; Harvati et al., 2003; Rosas et al., 2006), this space has been normally overlooked in paleoanthropology. Microcomputed tomography (microCT) allows the visualization of internal dental structures through the nondestructive production of virtual planes of sections facilitating the preservation and study of valuable fossil and museum collections (e.g. Kono, 2004; Tafforeau, 2004; Olejniczak and Grine, 2006). Only recently, some studies of the 3-D hominin pulp cavity proportions have been performed using microtomography (e.g. Bayle et al., 2009a, b, 2010; Crevecoeur et al., 2010; Kupczik and Hublin, 2010).

This technology gives a new perspective for the study of highly destructed fossil teeth, with crowns missing, high categories of wear, roots covered with hypercementosis or affected by taphonomic processes. This advantage has a special relevance when we are dealing with very limited and valuable fossil samples. This is the case of ATE9-1 specimen from the Sima del Elefante locality (Atapuerca, Spain). ATE9-1 was initially assigned to Homo antecessor (Carbonell et al., 2008), but this taxonomic classification was later revised, and this specimen was ascribed to Homo sp. (Bermúdez de Castro et al., 2011). It represents the earliest hominin fossil found in Europe, dated to the Early Pleistocene (c.1.3 Myr) (Carbonell et al., 2008). In general, the teeth of ATE9-1 show primitive traits for the genus Homo, but also some similarities with the H. antecessor teeth from the nearby locality of Gran Dolina-TD6 (c. 900 kya) (Bermúdez de Castro et al., 2011). A deeper assessment of the phylogenetic meaning of ATE9-1 root morphology can be found in Bermúdez de Castro et al. (2011).

The dental remains from ATE9-1 are fragmented. Only two crowns (LP4 and RI2) are preserved but they show a high category of wear, and all the roots evince a high degree of hypercementosis that avoid accurate external descriptions (Martinón-Torres et al., 2011).

The aim of the present study is to elaborate a detailed description of the ATE9-1 dental roots, extracting the maximum level of morphological information from these fragmented dental remains to make future comparisons possible. The external and internal morphology of the roots have been compared and the symmetry between antimeres evaluated to observe biological questions that have not been analyzed before in the roots and root canals by means of these relatively new technologies.

The Sima Del Elefante Site

During the 2007 field season, a hominin mandibular fragment (ATE9-1) was recovered from the TE9 level of Sima del Elefante cave site (TE), one of the Pleistocene sites from Sierra de Atapuerca (Burgos, northern Spain) (Carbonell et al., 2008). This site is located in the Railway Trench, 100 m from its entrance and about 200 m away from the well-known Atapuerca-TD site, the infilling of the Gran Dolina cave (Bermúdez de Castro et al., 1999). The TE site corresponds to a sedimentary karstic infilling stopping up the entrance to the so-called ‘Galería Baja,’ which belongs to the Cueva Mayor-Cueva del Silo complex, where the Sima de los Huesos site is located (Figure 1).

Previous field research at TE was devoted to cleaning and preparation of a vertical profile of the infilling to perform a detailed study of the lithological and sedimentary stratigraphical sequence (Rosas et al., 2001). During the 1980s, sedimentary samples for the biostratigraphical study of the Atapuerca sites (including TE) were obtained (Gil, 1987). However, a detailed, more recent and complete biostratigraphical study has been made by Cuenca-Bescós and García (2007). The Sima del Elefante cave is about 18 m wide and the railway outcrop exhibits a sedimentary thickness of about 24 m formed by 22 lithostratigraphic units mostly made by debris flow deposits (see Figure 1 of Carbonell et al., 2008). The TE9–TE14 levels have yielded an assemblage of Mode 1 lithic tools (Parés et al., 2006; Carbonell et al., 2008) and level TE9, in particular, presents an unexcavated area of more than 60 m². The lithic assemblage found at this level, a simple Mode 1 technology, shows similar primary technical features to those recovered from other Early Pleistocene European sites (Carbonell et al., 2008). Paleomagnetic analyses by Parés et al. (2006) revealed that a major geomagnetic reversal occurs between stratigraphic levels TE16 and TE17. This reversal has been interpreted as the Matuyama Chron, in consonance with the micromammal assemblage found at the site (Laplana and Cuenca-Bescós, 2000). Furthermore, levels TE9–TE13 display reverse magnetic polarity. The age of TE9 is further confirmed by burial dating based on the radioactive decay of cosmogenic $^{26}$Al ($t_{1/2} = 0.717 \pm 0.017 \text{ Ma}$) and $^{10}$Be ($t_{1/2} = 1.34 \pm 0.07 \text{ Ma}$) in quartz collected from the sediments (Carbonell et al., 2008). Thus, based on a combination of paleomagnetism, cosmogenic nuclides, and biostratigraphical data, TE9 level has been dated to the Early Pleistocene (c. 1.2 Ma) or possibly even older (1.3 Ma, Parés, personal communication).

Materials and Methods

Materials

The mandible preserves in situ the roots of lower left lateral incisor (LI2), lower right first premolar (RP3), and
lower right second premolar (RP4), and the apices of both lower right lateral incisor (RI2) and lower right canine (RC).

In addition, five isolated teeth were found in the same excavation square: the lower left second premolar (LP4), the root and the crown of the RI2, the root and fragment of the crown of the RC, a partial root which was initially classified as the lower left first premolar (LP3), and a root with a small fragment of the crown that was initially classified as a left canine (LC) (Table 1). Dental dimensions, the similar high degree of occlusal and interproximal wear, and the appropriate fit between the preserved part of the alveolus and the teeth suggest that they belong to ATE9-1.

Methods

The external morphology of the preserved isolated roots was assessed by visual inspection and it was classified according to Wood et al. (1988), which categorizes the root forms into four distinct groups: 1R, 2T (Tomes’ root), 2R (mesiobuccal and distal) and 2R (mesial and distal). 1R was defined as a single root with a single (main) canal (single roots of Tomes’ root form are included in this category). Two roots: Tomes’ root (2T) in which the grooves at the surface of the root led to bifurcation. The roots are mesiobuccal and distolingual, the mesial area of the distolingual root overlaps the distal area of the mesiobuccal root. Each root has a separate pulp canal.

Tomes (1923) was the first to describe this root structure in modern human P3s as a deviation from the normal European single oblong root. Heterogeneity was identified in a phenotype with some premolars being C-shaped in root transverse section (due to the unilateral induction of an interradicular process forming a prominent mesial/lingual groove), and others showing two root elements (relatively independent mesial/buccal and distal/lingual roots). Turner et al. (1991) normalized the continuous nature of the root structure of Tomes (1923). In this study, the classification of the Tomes’ root degrees was done following Turner et al. (1991). The primary elements of the root complex are root cones and radicular structures. The term radical will be used to refer to unseparated root-like divisions (Scott and Turner, 1997), when no true external bifurcation occurs. One root can have two or more radicals. If they are not separated, developmental grooves delimit the boundaries of these radicals. When the radicals are bifurcated, the teeth may have two or more roots (Scott and Turner, 1997).

The internal morphology of the roots (pulp cavity) of the ATE9-1 specimen and the external morphology of the in situ roots were analyzed by means of CT and microCT. ATE9-1 (Figure 2) suffered several post-depositional alterations, most of which were restored at the National Research Centre on Human Evolution (CENIEH) Conservation and Restoration Department. A fragment of the distal aspect of the right corpus including the distal wall of the RP4 socket was found separately. The RP4 was first recovered as a loose tooth and later included in its restored socket (Martinón-Torres et al., 2011). The scanning process was performed after the restoration work. Microtomography could only be done in the teeth that remained isolated after the restoration process (lower left premolars, both lower canines and lower right incisor) (Table 1).
The whole mandible was scanned using an YXLON MU 2000-CT scanner at the University of Burgos (Spain) using the following parameters: voltage = 160 kV, amperage = 4 mA, and a resultant voxel size of 0.5 mm × 0.5 mm × 0.5 mm. All the isolated teeth were scanned with a Scanco microtomographic system (µCT 80, Scanco Medical, Switzerland) housed at the National Research Centre for Human Evolution (CENIEH) using the following settings for each scan: voltage = 70 kV, amperage = 140 mA, and resultant voxel size = 20 mm × 20 mm × 20 µm). The images resulting from the CT and microCT scanning were cropped threedimensionally with the ImageJ software package (National Institutes of Health, USA) to eliminate background space and reduce the file size. Each of the microCT data files was filtered using a three-dimensional median filter, followed by a mean of least variance filter. These processes were performed to facilitate dental tissue segmentation. Following filtering of the image stack, the external tissues of the tooth and the pulp cavity of each tooth were segmented using a semi-automatic threshold-based approach with the Mimics software package v. 13.1 (Materialise, Belgium). The segmentation of the root canals had to be done mostly manually from the middle or apical third of the roots in all cases due to the deposition of matrix inside the canals in multiple locations. It was not possible to segment the cementum incremental layers of either the root or the secondary or tertiary dentine deposition layers.

For the description of the root canals the method described by Canalda and Brau (2006) was followed. This thorough and systematic method allows detailed anatomical descriptions of the root canals starting from the crown (that encompasses the pulp chamber) and following by the coronal, middle, and apical thirds of the root. In the ATE9-1 specimen, not all these parts were preserved in all teeth. All the descriptions are presented by antimeres to facilitate the assessment of asymmetry.

Measurements of the roots were taken only from the teeth with complete roots of the sample, LP4 and LI2. Proper landmarks could not be acquired from the rest of the root fragments to enable measurement of the complete root. The volume of the root (Rvol), the surface area of the root (Rsf), the volume of the radicular canal (Rpulpvol), the surface area of the radicular canal (Rpulpsf), and the root length (Rlength) were measured.
Results

Table 1 shows the location and preservation state of all teeth, the imaging method that has been used for each of them, and a summary of the results of the internal and external morphological analyses.

The portion of the in situ preserved fragment of the LI2 (Figure 3) is a single root without external bifurcation (1R of Wood et al., 1988). This root would be also classified as grade 0 of Tomes’ root according to Turner et al. (1991) with no external visible groove. However, internally we observe a possible bifurcation. A buccal and a lingual canal can be observed at the coronal third of the root in the tomography. They could be the result of a bifurcation of the main canal or they could be two separate canals. The lower resolution of the CT prevents us from seeing whether the lingual canal continues to the apex, since it disappears from the image at the middle third of the root. The buccal canal has a lingual bifurcation at the apex showing an oblique accessory canal (45° angle from the main canal towards the apex). The transverse sections of the root canals are circular over their entire length. The measurements of the LI2 root are contained in Table 2.

The RI2 root (Figure 4) is single (category 1R of Wood et al., 1988), distally deviated in its apical third and without evident developmental grooves, grade 0 of Tomes’ root following Turner et al. (1991). However, the CT reveals two rounded depressions in the external mesial and distal surfaces. 

Figure 2. Anterior view of ATE9-1 mandible (above) and anterior view of ATE9-1 mandible and in situ teeth based on computed tomographic reconstruction (below). The mandibular bone has been rendered semi-transparent to illustrate the position of the in situ teeth (coloured in blue).

Figure 3. Consecutive high-resolution medical CT transverse cross-sections of ATE9-1 demonstrating root morphology of the in situ dentition: (A) At the level of the cement–enamel junction (CEJ); (B) one-quarter of the distance from the CEJ to the root apex; (C) one-half of the distance from the CEJ to the root apex; (D) three-quarters of the distance to the root apex.
at the apical third that delineate a figure-of-eight-shaped section. The main root canal follows the straight trajectory of the root. At the apex, the main canal is divided into a buccal and lingual canal. The lingual canal bifurcates at the apex into a buccal and distal canal. The buccal apical canal is the largest, so its foramen could be considered the main foramen of the tooth. The longitudinal section of the main root canal is convergent to the apex. The transverse cross-section of the upper third of the root canal shows a circular shape. The apical third of the pulp cavity shows an elliptical shape that continues to the bifurcation of the canal at the apex.

The poor preservation of the LC (Figure 5) prevents an accurate assessment of its original external and internal morphology; only the apical third of the root and the pulp cavity could be visualized and examined. Based on purely external analysis, this root would be classified as 1R (Wood et al., 1988). It shows two shallow developmental grooves in the

<table>
<thead>
<tr>
<th></th>
<th>L12</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Rvol (mm$^3$)</td>
<td>Rsf (mm$^3$)</td>
<td>Rpulv (mm$^3$)</td>
<td>Rpulp (mm$^3$)</td>
<td>Rlength (mm)</td>
</tr>
<tr>
<td>LI2</td>
<td>336.42</td>
<td>445.37</td>
<td>6.97</td>
<td>52.24</td>
<td>16.42</td>
</tr>
<tr>
<td>LP4</td>
<td>641.7</td>
<td>548.41</td>
<td>21.31</td>
<td>82.45</td>
<td>18.46</td>
</tr>
</tbody>
</table>

Figure 4. (A) Buccal aspect of the RI2, external and internal (virtual filling of the pulp cavity) views. (B) Mesial aspect of the RI2, external and internal (virtual filling of the pulp cavity) views. (C) MicroCT cross-sections of the roots of the RI2 at the cervical, mid-height, and apical thirds.

Figure 5. (A) Buccal aspect of the LC, external and internal (virtual filling of the pulp cavity) views. (B) Mesial aspect of the LC, external and internal (virtual filling of the pulp cavity) views. (C) MicroCT cross-sections of the roots of the LC at the cervical, mid-height, and apical thirds.
mesial and distal surfaces of its apical third that delimitate a
distobuccal and mesiolingual component (grade 1 of Tomes’
root according to Turner et al., 1991) and a slightly bifid tip.
The CT transverse cross-sections of the external morpholo-
gy of the root also show the developmental grooves. The
mesiolingual radical is predominant at the apical third, and it
is slightly deviated to mesial. Four root canals (following a
buccolingual line) can be observed at the mid-third of the
root. They could be accessory ramifications of a main canal,
or this could be an indication that this canine had four sepa-
rated canals. These four canals are converted into three ca-
nals as they get close to the root apex where a ramification of
the root canals can be observed with no visible main canal or
foramen. This tooth was classified in previous studies as a
LP3 (Carbonell et al., 2008; Bermúdez de Castro et al.,
2011; Martínón-Torres et al., 2011). In this analysis, and in
light of the CT and microCT information, a new classifica-
tion is suggested (see below).

The RC (Figure 6) root is single and mesiodistally com-
pressed. Externally it would be classified as 1R (Wood et al.,
1988). Below the excess of cement we can observe mesial
and distal wide constrictions. The coronal half of the root
is composed of a main canal with a circular transverse profile,
which takes an elliptical shape just before dividing into four
accessory canals. It displays a straight trajectory, following
the shape of the root. The main canal divides into four smal-
er accessory canals that intertwine and end in a ramification
of the root canals where no main canal can be identified. The
longitudinal section of the main canal shows parallel walls.

Although there is a high degree of hypercementosis at the
apical third of the root of the LP3 (Figure 7), a light expres-
sion of a bifid tip could be observed. Based only on the ex-
ternal analysis of the morphology of this root, it could have
been classified as 1R (Wood et al., 1988). However, looking
at the internal and external morphologies it would be classi-
fied as double-rooted: 2T (Wood et al., 1988). There is a
moderately deep developmental groove in the mesiolingual
surface that extends along two-thirds of the total root length
(grade 3 of Tomes’ root according to Turner et al., 1991).
This groove delimitates externally a mesiobuccal and a dis-
tolingual radical. There is a main root canal which bifurcates
from the second third of the root, and from this point the
pulp cavity is composed of buccal and lingual canals which
remain separated until the apex. The canals follow the curve
of the root, without a strong angulation. The apices of
the root canals are curved, following the shape of the root.
There are two blind accessory canals whose trajectories end inside
the tooth, in this case in the cement. These accessory canals
start from the mesial and distal canals following an oblique
trajectory with a 45° angle. The apical third of the root canal
shows a ramification, and no main canal can be identified.

The apex is full of foramina with similar diameters. The
walls of the root canals in longitudinal section are parallel. A
transverse cross-section of the root canals at a cervical level
shows a circular shape. This tooth was previously classified
as LC (Carbonell et al., 2008; Bermúdez de Castro et al.,
2011; Martínón-Torres et al., 2011). In this analysis a new
classification is suggested (see below).

The external upper third of the transverse CT cross-
section of the root of the RP3 (Figure 3) is oval, with a slight
mesiolingual indentation. A mesiobuccal and a distolingual
radical are delimited externally by a moderately deep de-
velopmental groove in the mesiolingual surface that extends
along two-thirds of the total root length (grade 3 of Tomes’
root according to Turner et al., 1991). Internally, the main
root canal is bifurcated at the coronal third in mesiobuccal
and distolingual ramifications that continue as two separated
canals until the apex (Figure 3). The transverse sections of
the root canals are circular along their whole length.

The root of the LP4 (Figure 8) is relatively straight with a
slight distal deviation. It presents a prismatic shape with four longitudinal external grooves (buccal, mesial, mesiolingual, and distal) which start at the second third of the root and get more pronounced towards the apex. Due to the shallow developmental grooves observed in the root surface, we would classify this tooth as grade 1 of Tomes’ root according to Turner et al. (1991). The generalized high level of hypercementosis present in the root of this tooth, as well as in the rest of ATE9-1 dentition (Martínón-Torres et al., 2011) makes it very difficult to describe the external anatomy of the root. Despite the external demarcation of four radicals, internally there is a single main root canal with bifurcation at the apical third so we would classify the LP4 root as 2T (Wood et al., 1988). A large pulp chamber with marked constriction at the floor, where the root canal starts, can be visualized. Internally, the root canals of this premolar (as well as in the rest of ATE9-1 teeth) were obliterated by means of post-mortem-deposited matrix and secondary dentine that is physiologically deposited through the life of the subjects (Benzer, 1948). At the apical third, the root canal is bifurcated and shows an apical ramification formed by a mesial and a distal canal that disappear and become multiple ramified...
collateral canals. At the apex, there is one foramen that could be distinguished from the others due to its larger diameter. It is located at the mesial part of the apex of the root, and it could be considered the main foramen of this radicular canal. The longitudinal section of the whole root canal is convergent towards the apex. In cross-section, the pulp chamber has a buccolingual ellipsoidal shape. The transverse cross-section of the root canal is rounded and the walls show some roughness which is likely due to post-mortem deposition of sediments inside the pulp cavity. The measurements of the LP4 root are provided in Table 2.

At the external apical third of the root of the RP4 (Figure 9) we can distinguish a mesiobuccal and a distolingual radicals separated by a deep distobuccal groove and a shallow mesiolingual one. The mesiobuccal cone is shorter and flexed. Despite the deep invagination at this level, the apex of this radical is fused to the distal radical. We could classify this root as grade 3 of Tomes’ root (Turner et al., 1991) due to the depth of the cleft. The transverse CT cross-sections (Figure 3) reveal that in its external coronal third the root is prismatic with four slight indentations, one buccal, one distal, one mesiolingual, and a shallower mesial one, similar to the left antimer. Attending to the CT images and the visual inspection, this root would be classified as 2T (Wood et al., 1988). Internally, the main canal is bifurcated into two canals at the apical third. A mesiobuccal and a lingual canal can be observed at the root apex. The cross-section of the root canal is circular throughout the whole length.

Discussion

The root surfaces of all of the teeth in ATE9-1 exhibit an irregular thickening and rough surface due to abnormal cementum deposition particularly affecting the apical third (Martinón-Torres et al., 2011). The excessive proliferation of cementum beyond the physiological limits of the tooth is called hypercementosis (Weinberger, 1954; Leider and Garbarino, 1987; Hillson, 2008; Pinheiro et al., 2008) and leads to the abnormal thickness of the root, predominantly near the apex which becomes rounder in shape (Pinheiro et al., 2008). The generalized hypercementosis observed in ATE9-1 prevents a proper assessment of the root external morphology and obliges to be cautious when recording measurements.

In previous assessments of the Sima del Elefante mandible (Carbonell et al., 2008; Bermúdez de Castro et al., 2011; Martinón-Torres et al., 2011), a different classification of the mandibular teeth was suggested. LC (in this study) was identified as a LP3, and vice versa. After the analysis of the morphology of the roots and the root canals of ATE9-1 the classification of the teeth was reconsidered due to several reasons. The buccal outline of the preserved crown of the LP3 (Figure 7b) was too rounded to be a canine. Buccal surfaces in lower premolars tend to be more semicircular (Diamond, 1962; Woelfel and Scheid, 1998; Riojas, 2006), as is the case of the root fragment designated as a LP3 in this study and that it is similar to the buccal outline of the LP4 (Figure 8b). With this new classification, the transverse sections of the LP3 (Figure 7c) and the RP3 (Figure 3) are highly coincident. This fact contradicts previous statements about strong asymmetry between antimeres (Bermúdez de Castro et al., 2011). LC would still present a grade 1 of Tomes’ root though this trait is absent in the RC. Interestingly, the external root morphology of ATE9-1 P3s is now identical to the root morphology described for H. antecessor P3s, and that was suggested as possibly apomorphic for this species (Bermúdez de Castro et al., 1999).

The existence of an abscess in the LC alveolus (Martinón-Torres et al., 2011) has remodeled the distal wall of the socket, creating a space between the tooth and the socket and making relatively good fitting of both pieces in the same socket. Finally, and under this new possibility, we have noted that there is a good fitting between the mesial interproximal facet of the LP4 and the small preserved portion of the distal interproximal facet of the LP3.

ATE9-1 roots present relatively complex external and internal root systems. There is neither a general nor straightforward correspondence between the external root morphology and the root canal’s morphology. From the early studies of Hess and Zürcher (1925) on modern human samples, the anatomical complexity of root canals is becoming increasingly documented (e.g. Cleghorn et al., 2007a, b). It is known that a root with a single conical canal with a single apical foramen is not the typical morphology but rather the exception (Cohen and Burns, 2002; Vertucci, 2005). The frequency of multiple foramina, accessory canals, and other anatomical variations in root canals demonstrates that such morphology is so frequent that it must be considered the normal anatomical condition (Cohen and Burns, 2002). With a normal degree of variability, particularly in ‘minor variants’ such as the number of foramina or the accessory canals, most teeth are expected to show a somewhat consistent pattern in their root canal morphologies (Tronstad, 1993). Looking at the teeth of ATE9-1, we can see examples of a high morphological degree of internal–external variation with lack of concordance between the number of radicals and root canals (see Table 1). This is the case of LI2 (1R with two separated canals from the coronal third: see Figure 3), LP3 (2T that shows two clearly separated canals from the coronal third: see Figure 5) and RP3 (2T with two clearly separated canal from the coronal third: see Figure 3).
The external surfaces of the roots are affected by the environmental and life conditions of individuals. The generalized hypercementosis of all the ATE9-1 teeth has been related to excessive movement of the tooth within the socket in a first stage and/or to a high compensatory eruption rate due to a lack of proper opposing teeth (Martínón-Torres et al., 2011). Nevertheless, the root canals are more stable and not so affected by external factors. This is why, in our opinion, the morphology of the root canals is more reliable in this case and complementary to the external root morphology, especially in the case of ATE9-1, where a high degree of hypercementosis is present.

In summary, it has been demonstrated that in cases where a high degree of destruction and hypercementosis are present in a fossil, the apparent external morphology of the roots can be highly confusing. In these cases, tomographic and microtomographic techniques are fundamental to get a clear idea of the external and internal morphology of the teeth and to obtain a significant amount of biological information that otherwise would have been unavailable. A new classification of two of the ATE9-1 teeth was performed relying on the tomographic and microtomographic images and the analysis of the original fossil. Classically, we have relied on the external identification of roots and radicals to characterize hominins and assess their phylogenetic proximity/distance (e.g. Scott and Turner, 1997; Irish and Guatelli-Steinberg, 2003). In this study it has been demonstrated that the internal root anatomy could be used as a complementary source of biological information. The classification of LP3 and LC has been modified after the analysis of the internal morphology of the teeth by tomographic and microtomographic images; this lead to the conclusion that the internal root anatomy could be used as a complementary and more reliable source of biological information.

Acknowledgments

This study was made possible by financial support from the Fundación Atapuerca, the Spanish Ministry of Science and Innovation, and the Junta de Castilla y León (Project number CGL2009-12703-C03-01, Proyecto Grupo de Excelencia de la Junta de Castilla y León GR249). This study benefited greatly from contributions by the following individuals and institutions: the University of Granada, the University of Burgos, with special thanks to Laura Rodríguez and Elena Santos. Thank you to Simon Henchy for his invaluable help with English corrections. Special thanks should be also given to Pilar Fernández-Colón and Lena Lacasa-Marquina from the Conservation and Restoration department of CENIEH (Burgos) and the Atapuerca excavation and research team. Thank you to Dr Bayle for her revision which has helped to improve the quality this paper. We also thank Dr Kono for her invaluable insights into ATE9-1 dental morphology. Thank you very much to Dr Hanihara and the anonymous associated editor for their suggestions and corrections which helped to improved the paper significantly. And thanks to Luis Tortosa Santiago for his valuable technical help.

References


Cuenca-Bescós G. and García N. (2007) Biostratigraphic succession of the Early and Middle Pleistocene mammal faunas of
the Atapuerca cave sites (Burgos, Spain). Cour Forsch-Inst Senckenberg, 259: 99–110.


