A Middle Pleistocene fossil hominin maxilla from the Republic of Djibouti (East Africa)

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Abstract
The HRD1 hominin maxilla was discovered during fieldwork carried out in the Republic of Djibouti, eastern Africa, in the 1980s. The HRD1 specimen is attributed to the genus Homo and has been dated from the Early to the Middle Pleistocene. This paper presents a detailed morphological and quantitative description of the HRD1 maxilla. The morphology of the dental roots, the enamel thickness, the morphological architecture of the premaxillary—maxillary complex, and the morphology of the maxillary sinus were all examined, yielding the data provided here. The Djiboutian specimen represents one of the late Early to Middle Pleistocene occurrences of Homo in an area where Pleistocene hominins are poorly documented despite a relative abundance of lithic artefacts. However, the precise identification of the specimen remains challenging and requires additional comparative analysis.

Key words: Homo, east Africa, teeth, anatomy

Introduction
The position of Homo sapiens in the history of life and the phylogeny of hominines are major issues in paleoanthropological studies. The search for ancestors requires an extended knowledge of past populations. The fossil record is scarce and all fossil remains are therefore significant in this inquiry (Chauhan, 2009). This paper aims to further describe a hominin maxilla from the Pleistocene in the Republic of Djibouti.

The Republic of Djibouti is situated in eastern Africa between the Equator and the Tropic of Cancer, at the northern edge of the ‘Horn’ of Africa. It is surrounded by Eritrea to the north, Ethiopia to the west and south, and Somalia to the south, along the Bab-el-Mandeb straits that connect the Red Sea to the Gulf of Aden and on to the Indian Ocean (Figure 1). The landscape is hilly, especially in the north, with two lakes, Assal in the middle and Abhé in the southwest of the country. It is characterized by the presence of significant volcanic activity. The area is in the Afar Triple Junction, a triple tectonic plate junction between the Arabian, Somali, and Nubian tectonic plates. The Afar Rift constitutes the northern part of the great African Rift Valley (Courtillot et al., 1984; Vigny et al., 2007). The HRD1 specimen came from the southern part of the Republic in the Gobaad depression, which is overlaid by Pleistocene lacustrine and fluviatile deposits, in the Dikhil Basin. Rifting activity has resulted in occasional intercalations of basaltic or rhyolitic lava. The sediments contain fossil vertebrates that provide biochronological information on the level as well as the radiometric ages of the volcanic ashes or lava and also paleomagnetic data (de Bonis et al., 1984). Sen found HRD1 in the winter of 1983 during a field trip organized by the Universities of Paris 6 and Poitiers, the French CNRS, and the ISERST of Djibouti. The specimen is presently housed at iPHEP, University of Poitiers, and will soon be housed in the ISERST of Djibouti.

Geological Setting
Several researchers have studied the geology of the area. Dreyfuss (1932) provided an overview of the territory, reporting on volcanic rocks and on ammonites and other invertebrate fossils in Mesozoic sedimentary levels, and on freshwater shells in the Plio-Pleistocene deposits particularly in the Gobaad plain. He did not note any fossil bones. Similarly, Aubert de La Rüe (1939a, b) provided information focusing mainly on the volcanic rocks and a geographic description. Later, knowledge of the geology of Djibouti increased (Gasse and Rognon, 1973; Roger et al., 1974; Gasse, 1975; Gasse et al., 1980; Fournier et al., 1983) and the presence of fossil vertebrates was reported. Other contributions were
more focused on the fossil vertebrates and artefacts (de Bonis et al., 1984, 1988; Thomas et al., 1984; Geraads, 1985; Chavaillon et al., 1986, 1987, 1990; Berthelet et al., 1992; Faure and Guérin, 1997; Berthelet and Chavaillon, 2001; Berthelet, 2002). After a gap of several years, another team continued the field research (Harmand et al., 2009) but still no hominid remains were found. The fossil mammals unearthed during the course of all these field campaigns help to form a biostratigraphic frame for the deposits mainly in the Gobaad area. Several continental formations were delimited (Roger et al., 1974). Remains of a skeleton of *Elephas recki ileretensis* have been unearthed at the site of Barogali (Chavaillon et al., 1987) and dated from 1.3 to 1.6 Ma. Another *E. recki* has been found in the site of Haïdalo in the same area (Chavaillon et al., 1990) but belonging to the sub-species *E. r. recki*, younger than *ileretensis* and dated from 1.2 to 0.5 Ma. Finally, the human maxilla HRD1 studied in this paper was found at Haraïde (HRD1), a site about 6 miles north of As Eyla, on the banks of the ouadi Dagadlé (de Bonis et al., 1984; Chauhan, 2009; Harmand et al., 2009). The specimen was discovered in situ in a very small cliff, in a quite flat area, and therefore cannot come from an upper level. The presence of ancient hominids in the area of Djibouti was first mentioned when artifacts were collected from the surface (Teilhard de Chardin, 1930; Teilhard de Chardin et al., 1939–1940) and confirmed by most of the publications cited above. The discovery uncovered for the first time one of the toolmakers of the countless artifacts found in the the Republic of Djibouti. The maxilla comes from the same layer of greenish slaggy and clayish sands as that of the upper level of the close locality Barogali and therefore is more recent than the fossiliferous level of that locality which dates back at least to 1.3 Ma (Figure 2). The human fossil was found together with a rather poor mammalian fauna with equid sp., *Hippopotamus* of large size, and fragments of horn cores from a bovid similar to *Megalotragus* that are not significant enough to date the locality. Nevertheless, the presence of the suid *Metrichoerus compactus* and the derived *E. r. recki* provide a window to date the locality. The former species appeared in east Africa around 1.4 Ma and disappeared around 0.4 Ma (Cooke, 1985: fig. 3). In southern Africa it appeared around 1.1 Ma and is definitely found

![Figure 1. Map of the Republic of Djibouti. † Fossil locality.](image)

![Figure 2. Section of sedimentary deposits in the Gobaad near Barogali (modified from Berthelet, 2002). The arrow indicates the level of the maxilla HRD1. (a) Compacted gysiferous brown-greenish clays (2 m). Bones and artefacts were at mid-height cloaked by limestone crust including *Elephas recki ileretensis*. (b) More or less clayish orange sands (0.2 m). (c) Compacted brown clays, powdered at the top (2 m). (d) Greenish clays and greenish sands (1 m). The same sands are indicated as “scoriaceous sands” in Bonis et al. (1984). In Haraïde, this layer includes HRD1 maxilla, *Equus* sp., *Elephas r. recki*, *Hippopotamus* sp., *Megalotragus*, *Metrichoerus compactus*. (e) Sands and rare lava blocks: level of the upper lava flow (0.3–1 m). (f) After a stratigraphic gap, Holocene deposit of white diatomitic marls (2–3 m) with gastropod remains at the base. (g) Broken brown crust.](image)
until around 0.4 Ma and could possibly have been present until 0.15 Ma (Klein, 1984: table 3). Nevertheless Cooke (1985: 116) rather deliberately avoided correlation between the East African and South African deposits because there is a difference in the interpretation of the South African material." Metridiochernes compactus is found in North Africa around 0.8 Ma (Geraads, 2010). The remains of E. recki are identified as those of the sub-species E. r. recki as at the site of Haïdalo in the same area. This sub-species occurred in Africa between 1.2 and 0.5 Ma (Beden, 1979, 1985). Thus we can definitely place the age of the human maxilla between 1.2 Ma and 500 kyr.

Material and Methods

HRD1 is the left part of an undistorted, and highly mineralized, hominin maxilla with alveoli for the incisors and canine, a fragment of P3, and P4–M3. The tooth roots, in the maxillary bone, are well preserved. The intermaxillary suture is preserved from the incisors to the level of M2. The bottom of the nasal cavity and a large part of the maxillary sinus are visible but the higher portion of the nasoalveolar clivus is broken and the nasal spine and the prosthion are damaged. The full length of incisive canal is intact. The measurements of the teeth were made with a digital calliper accurate to 1/10 mm for the mesiodistal (MD) and buccolingual (BL) diameters (Wood, 1991; Benazzi et al., 2011). A sharpened point mechanical sliding calliper accurate to 1/10 mm measured the height of the crowns, using modified beaks in the same way as Mehta and Evans (1966: fig. 1). The crown area and the relative cusp area of M2 were computed following the procedure described in Quam et al. (2009) on the first molar. The specimen was scanned using a Ultraton Resolutions microtomograph with a 0.029 mm isovoxel size resolution. This allows access to inner structures such as root morphology. The teeth were isolated from the maxilla bone using semi-automatic segmentation. Three-dimensional enamel thickness (Guy et al., 2013) and lateral enamel thickness were measured (Suwa and Kono, 2005) on M2–M3. The tooth wear was estimated according to Broca and Dawson–Brown stages (Broca, 1879; Dawson and Brown, 2013) although the latter concerns lower milk teeth.

The reconstructed digital 3-D volume of the semi-maxilla was used to propose reconstitution of the specimen allowing an evaluation of the maxilla/palate breadth and depth.

Description

Maxilla

From a dorsal view (Figure 3a, c), the nasal cavity floor appears elongated, sagittally flat and mediolaterally slightly concave; the anterior part rises gently. The large bean-shaped maxillary sinus floor is apparent (Figure 3a, c). It is composed by two fossae, a large one anteriorly and a smaller, narrower one posteriorly. They are not separated by a wall but rather by a very low, barely noticeable crest. The floor of the anterior fossa has three small mediolaterally directed depressions and that of the posterior fossa has two smaller depressions. The floor of the sinus is very thin and the apices of some molar roots are exposed in the sinus. Nevertheless, there is great variation of sinus morphology and volume in extant Homo sapiens (Figure 4). The sinus may be long (a, d, g) or short (c), divided in three (d, f, g) or two (a) chambers or without clear division (b), invading (a, b, i) or not (d, f) the zygomatic arch.

The palate (Figure 3b, d) is quite complete from the tooth row to the intermaxillary suture; its general aspect is a part of a semi-elliptic regular curve, the incisor alveoli being slightly anterior to the bicanine line. The palate is characterized by its great depth with a stepped slope behind the incisors and vertical walls laterally. The morphology of the surface of the hard palate is rough, displaying several bumps and crests. The great palatine foramen is anteriorly prolonged by a marked groove with developed palatine spines.

In lateral view (Figure 3e, g), although the incisor alveoli are not complete, we can perceive that the incisor roots were almost vertical although the premaxilla shows a moderate alveolar prognathism. There is a very shallow and narrow depression just in front of the P3 root. The lateral surface is rough with a small depressed surface above M2. Roots appear through two fenestrations above P3 and M1. The lower part of the alveolar bone bulges slightly along the tooth row. The preserved lateral portion of the maxilla is 20 mm high above P3 and 11 mm above M3.

The medial view (Figure 3f, h–j) shows the sagittal section of the incisive canal separating the premaxilla from the hard palate. The canal is thin and obliquely directed, the premaxilla clearly overlaps the hard palate, the thickness of which does not vary anteriorly. In this respect, the incisive canal in HRD1 differs from the “anterior position of the incisive canal, which is nearly vertical” in H. antecessor, Neandertals, and modern humans (Arsuaga et al., 1999: 449, fig. 8; Franciscus, 2003: fig. 3; Martinón-Torres et al., 2007: 67).

Despite the erosion of part of the premaxilla, it seems than the step between the nasal floor and the premaxilla was weak or absent (McCollum et al., 1993; McCollum and Ward, 1997; Franciscus, 2003; Wu et al., 2012).

Overall, HRD1 is bigger than the maxilla of extant Homo sapiens and the anterior part of the premaxilla is less stepped. The palate roof is very deep, similar to that of the deepest modern human maxillae (Table 1, Figure 5). When compared to other representatives of Homo species, the depth of the palate is very great but there is a large range of variation in the genus (Murril, 1975; Vandermeersch, 1981).

Teeth

The anterior part of the premaxilla is damaged and the incisor alveoli are open. The I1 socket is quite deep (about 14 mm) and that of the I2 is estimated to be 11 mm. The canine alveolus is large and oval, being slightly mesiodistally compressed (mesiodistal: 5.2 mm; buccolingual: 8.3 mm), with a depth estimated at 18.7 mm. The P3 crown is only present through a piece of dentine and enamel in the distobuccal corner. The occlusal surface of P3 is worn out and it is impossible to distinguish a detail (Broca stage 4, Dawson–Brown stage 9) and therefore impossible to know if there was a longitudinal fissure. The enamel is partially missing from the lingual face but it is possible to get the mesiodistal and buccolingual measurements at the cervix. There are no Carabelli or Bolk’s tubercles in the molars. If we take into
account the size, we obtain for the mesiodistal diameter $M_1 < M_2 > M_3$, for the buccolingual diameter $M_1 > M_2 < M_3$, and for the crown area ($MD \times BL$) $M_1 < M_2 > M_3$ (Table 1). $M_1$, of which the mesiolingual part of the crown juts out, has a rectangular buccolingually extended occlusal profile. It is heavily worn and the cusps are not visible (Broca stage 3, Dawson–Brown stage 8); the enamel is preserved only at the cervix and on the distobuccal side. The mesiodistal diameter of the tooth is certainly slightly reduced by wear (Mehta and Evans, 1966). $M_2$ is significantly less worn (Broca stage 1, Dawson–Brown stage 3), and does not display dentine spots. A piece of enamel is missing in the distolingual corner with a part of the hypocone. The occlusal outline is heart-shaped, the lingual half being slightly reduced. The paracone is larger than the metacone, the latter being slightly more worn. The hypocone, of which the distolingual corner is missing, would have been slightly smaller than the metacone. The protocone is not directly in contact with the metacone but connects through a central bean-shaped depression. The paracone is the larger cusp of the tooth although this is usually the case for the protocone (Table 1) (Quam et al., 2009; Bailey, 2004). A mesial cingulum runs from the paracone to the mesiolingual corner of the crown. $M_3$ is the smallest molar. Its occlusal outline is oval. It is fresh and has an unusual occlusal pattern. A large deep central basin is surrounded by a crenulated crest along the edges of the crown. The main cusps, paracone, protocone, and hypocone of the crown are hardly distinguishable, the metacone being replaced by several cusplets. There is a small low mesial cingulum. The surface of the enamel displays multiple small indentations that are evidence of hypoplasia (Ogden, 2008). There is no trace of dental caries in the HRD1 dentition.

The 3D average enamel thickness is 1.2 mm on $M_2$ and 1.3 mm on $M_3$ while lateral enamel thickness remains in the range of modern human thickness for both molars (Figure 6) (Suwa and Kono, 2005).
Figure 5. HRD1: (a) dorsal view of mirror reconstructed maxilla; (b) anterodorsal view; (c) palatal view; (d) coronal section at the level of M2 of the reconstructed virtual maxilla.

Figure 6. HRD1: (a) perspective view of the tooth row showing the molar enamel thickness variation, from 0.2 mm (blue) to 1.8 mm (red); (b, c) lateral enamel thickness measurements (solid line) on M2 (upper row) and M3 (lower row).

Figure 7. (a) Palatal view of the HRD1 maxilla showing the virtual sections along the tooth row; (b–d) parasagittal slices (medial to lateral) of the tooth row; (e–g) lingual, buccal, and apical view of the teeth showing root number and morphology.
**Dental diameters**

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<th>P4</th>
<th>M1</th>
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<tr>
<td>MD</td>
<td>7</td>
<td>10</td>
<td>11</td>
<td>9.8</td>
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<tr>
<td>BL</td>
<td>10</td>
<td>13</td>
<td>13</td>
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**Cusp size and proportion**

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<thead>
<tr>
<th></th>
<th>mm²</th>
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<tr>
<td>Paracone</td>
<td>36.7</td>
<td>29.2</td>
</tr>
<tr>
<td>Metacone</td>
<td>31.1</td>
<td>24.7</td>
</tr>
<tr>
<td>Protocone</td>
<td>31.9</td>
<td>25.3</td>
</tr>
<tr>
<td>Hypocone</td>
<td>26.2</td>
<td>20.8</td>
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<td></td>
<td>125.9</td>
<td>100</td>
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**Maxilla dimensions**

- **Tooth row length (P₃)–M₃** (44.2)sm
- **Molar row length M₁–M₃** 31.1
- **Canine alveolus breadth** 5.2
- **Palatal length** (48)sp.
- **Palatal depth at M₂** 19

**Width of the maxilla at the level of**

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<thead>
<tr>
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<th>P3</th>
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<th>M1</th>
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<tr>
<td></td>
<td>47.1</td>
<td>48.9</td>
<td>57.3</td>
<td>60.7</td>
<td>58.3</td>
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**Width of the palate at the level of**

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<th></th>
<th>P3</th>
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<tr>
<td></td>
<td>—</td>
<td>30</td>
<td>32.3</td>
<td>35.9</td>
<td>34.3</td>
</tr>
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1 MD, mesiodistal; BL, buccolingual (see Wood, 1991).
2 See Quam et al. (2009).
3 est., estimated.

**Dental roots**

There is no taurodontism in the dentition and the pulp cavities do not invade the roots (Figure 7). All the roots from P₃ to M₃ are visible in 3D (Figure 7). P₄ has two roots of about the same length and fused from the crown to mid-height level. The lingual root is cylindrical tapering around the apex and slightly distally hooked, while the more robust buccal root is flattened mesiodistally and slightly lingually hooked. There are two canals as is the case in most Homo sapiens (Kartal et al., 1998). The two roots of P₄ are fused except at their apices. They are distinguished by two vertical grooves, mesial and distal, the latter being more marked. There is only one canal as is the case in 50% of extant populations (Kartal et al., 1998). The single M₁ lingual root is large and flattened buccolingually with a very shallow groove from the base to mid-height; the two buccal roots are shorter than the lingual root, quite cylindrical and well separated. The buccal palatal roots spread 28° (Smith et al., 2009), which is within the range of Homo sapiens. M₂ and M₃ have an unusual pattern with four roots. The M₂ lingual root is similar to that of M₁ but without any buccal groove. The lingual roots are closer together and the mesial root is extended buccolingually. The base of the mesial root is fused to the lingual root with a vertical mesial groove and two separated apices indicating two roots. The apices of the distobuccal and lingual roots are not completely closed, probably indicating a recent eruption. Similarly all the M₃ root apices are still open (Figure 7g). The buccal, central, and mesiolingual roots are fused while the distolingual is separate. We note that the posterior root of M₂ and the mesial root of M₃ protrude slightly through the thin floor into the sinus but the sinus is not curved (see Sharan and Madjar, 2006: fig. 2).

**Conclusion**

The Djiboutian specimen therefore represents one of the Late–Early to Middle Pleistocene African occurrences of Homo. The presence of HRD1 in Djibouti is very significant in an area where Pleistocene hominins are poorly documented despite a relative abundance of lithic artefacts. However, it is very difficult to precisely identify the specimen given that it is incomplete and caution must be the rule in interpreting paleoanthropological results.

**Acknowledgments**

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**References**


