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The Late Pleistocene human dental remains from Mandrin Cave, France

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Mandrin Cave, located in the southeast of France, near the town of Malataverne, overlooks the eastern bank of the middle Rhône River Valley at an elevation of 225 m. Since 1990, excavations have revealed a 3-m deep stratigraphic sequence containing 12 archeological layers (layers J to B) ranging from marine isotope stage (MIS) 5 to the very end of the Middle Paleolithic, and the emergence of the Upper Paleolithic [1-2]. In nearly all of these layers, except H and J, dentognathic specimens (mostly isolated teeth) belonging to *Homo* were identified so far. Layers I, G and F, dating from ~80 to 60 ka, yielded Mousterian industries and three fragmentary deciduous and permanent tooth crowns (Man15 G 2851, Man15 G 2852, Man21 F 1139), as well as one LLdm2 (Man19 I 948) and one LLM1 (Man98 F 811). Layer E, dated to ~54 ka, marks a radical transition in the archeological sequence, with blades, bladelets and small points belonging to the Neronian culture, which shows manifest similarities with Initial Upper Paleolithic industries from western Asia. Within the well-constrained Neronian Layer E, an URdm2 was found (Man12 E 1300) [2]. The three overlying archeological levels contain Mousterian industries, together with two isolated URdm2 (Man04 D 395, Man04 D 679) in layer D (dated to ~53 ka), a LLdm2 and a LLM3 (Man02 C 983, Man11 C 204) in layer C (dated to ~51 ka), and portions of a mandible and maxilla with 31 permanent teeth belonging to a single individual nicknamed Thorin in layer B (dated to ~50 ka). This nearly complete dentition lacks the ULC, URp3 and URp4, but includes two supernumerary lower molars (LLM4 and LRM4). In total, 41 human dental elements spanning the stratigraphic sequence of Mandrin Cave were studied, representing a minimum of nine individuals, five juvenile Neanderthals, a modern human child and three adult Neanderthals. We analyzed the microCT record of the human teeth and investigated the external and internal structure, including the enamel-dentine junction (EDJ) that is a reliable taxonomic proxy [2], and compared these data with those available for Neanderthals, Late Pleistocene modern humans, and Holocene humans. Among the layer I–F teeth, the better preserved LLdm2 and LLM1 exhibit a complete mid-trigonid crest at the EDJ level and geometric morphometrics indicate that they both have a typical Neanderthal shape [2]. Geometric morphometric analyses of the EDJ shape and talon outline of the Layer E URdm2 unambiguously attribute it to an Upper Paleolithic modern human. Shape analyses of the crown outline of the isolated URdm2s from layer D and of the LLdm2 of layer C show that they belong to Neanderthal children. The morphology of the sub-complete dentition of Thorin from layer B exhibits typical Neanderthal features, with shovel-shaped maxillary central incisors, marked labial convexity on the maxillary lateral incisors that also show a large tuberculum dentale on the lingual aspect of the crown, a well-developed hypocone projected lingually in the maxillary molars, and high root stem/branches ratio (i.e., taurodontism). The presence of the two distomolars is outstanding as they are extremely rare in living humans (around 0.02%) and, to the best of our knowledge, have not been reported in Pleistocene *Homo* so far, though a few occurrences of other kinds of supernumerary teeth have been described in Neanderthal and Paleolithic modern humans [3]. Studies of odontoskeletal anomalies found in early-generation hybrids of living primates display a relatively high incidence of distomolars [4]. Considering that an early incursion of modern humans is recorded at Mandrin Cave ~54 ka and that dispersals are recorded around 48–45 ka [5], it is possible that interbreeding occurred in the region ~50 ka. The site of Mandrin Cave is remarkable as it documents the first alternating occupation of Neanderthals and modern humans, as well as a unique record of various Neanderthal groups during most of the Late Pleistocene.

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