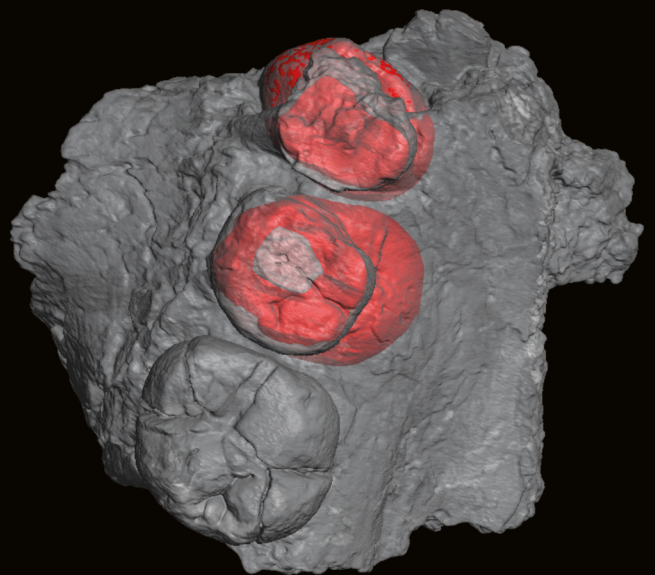


**New insights into the ontogeny
of *Paranthropus boisei* offered by a juvenile maxilla
from the Shungura Formation (Ethiopia)**

Arthur THIEBAUT, Franck GUY, Leslea J. HLUSKO,
Jérôme SURAULT, Ian TOWLE, Blade E. REDAE & Jean-Renaud BOISSERIE



**GLIMPSES OF A PLIO-PLEISTOCENE AFRICAN ECOSYSTEM:
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New insights into the ontogeny of *Paranthropus boisei* offered by a juvenile maxilla from the Shungura Formation (Ethiopia)

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ABSTRACT

Early hominin juvenile fossils are key for elucidating the developmental basis of adult phenotypic variation and enhancing our understanding of phylogenetic relationships. Since the discovery of the Taung child a century ago, numerous findings have expanded our knowledge concerning craniodental ontogeny of *Australopithecus africanus* and *A. afarensis*, and more recently, *Paranthropus robustus*. However, less is known about the derived, robust species *P. boisei* from eastern African. In this study, we present a juvenile maxilla specimen of *P. boisei* recently recovered from the Shungura Formation (Ethiopia), offering insights into the craniodental development of eastern African robust hominins. To give an age at death, the dental developmental stage was studied and compared to those of *P. robustus* individuals. We then examined the expression of derived morphological features, comparing them to those observed in various published fossils, in order to explore the craniofacial ontogeny of the genus *Paranthropus*. Our results show that OMO 362-10001 age at death is estimated to have been around 3.8 to 5 years old. The OMO 362-10001 maxillary morphology indicates that some of the derived features shared by species of the genus *Paranthropus* are already evident by this stage of development while others are not. This present ontogenetic pattern differs in some way from that of *P. robustus*, suggesting ontogenetic variation within the clade *Paranthropus*.

KEY WORDS

Fossils,
robust hominins,
facial morphology,
dentition.

RÉSUMÉ

Nouvelles perspectives sur l'ontogénie de Paranthropus boisei à partir d'un maxillaire juvénile de la formation de Shungura (Éthiopie).

Les fossiles juvéniles d'hominines sont essentiels pour éclairer les bases ontogénétiques responsables de la variation phénotypique adulte et pour affiner notre compréhension des relations phylogénétiques. Depuis la découverte de l'enfant de Taung il y a un siècle, de nombreuses découvertes ont enrichi nos connaissances sur l'ontogénèse craniodentaire d'*Australopithecus africanus* et d'*A. afarensis*, ainsi que, plus récemment, de *Paranthropus robustus*. En revanche, la croissance et le développement de *P. boisei*, un hominine robuste dérivé d'Afrique de l'Est, demeurent bien moins documentés. Dans cette étude, nous présentons un spécimen juvénile de *P. boisei* récemment découvert dans la formation de Shungura (Éthiopie), offrant de nouvelles perspectives sur le développement craniodentaire des hominines robustes est-africains. L'âge au décès a été estimé à partir du stade de développement dentaire, en le comparant à celui d'individus juvéniles de *P. robustus*. Nous avons ensuite examiné l'expression des caractères morphologiques dérivés chez l'individu étudié, en les comparant à ceux observés sur divers fossiles publiés, afin d'explorer l'ontogénèse cranio-faciale du genre *Paranthropus*. Nos résultats indiquent que l'âge au décès de l'individu OMO 362-10001 se situe entre 3,8 et 5 ans. La morphologie maxillaire de ce spécimen révèle que certains traits dérivés partagés par les espèces du genre *Paranthropus* sont déjà présents à ce stade du développement, tandis que d'autres ne le sont pas encore. Ce schéma ontogénétique diffère en certains points de celui observé chez *P. robustus*, suggérant une variation de pattern ontogénétique au sein du clade *Paranthropus*.

MOTS CLÉS

Fossiles,
hominines robustes,
morphologie faciale,
dentition.

INTRODUCTION

The Early Pleistocene robust hominins, often categorized taxonomically as the genus *Paranthropus* (*P. robustus*, *P. boisei*, and *P. aethiopicus*), exhibit distinctive craniofacial characteristics. Compared to geologically older hominins, these derived anatomical features include a retracted flat face (orthognathic), anteriorly positioned zygomatic processes, and a cranio-caudally thick and deep palate (Rak 1983; McCollum 1999). These shared characteristics are often interpreted as shared-derived traits within the genus (Wood & Constantino 2007; Mongle *et al.* 2023).

Juvenile fossil specimens provide significant insights into the developmental patterns underlying adult phenotypic variation (Jeffery *et al.* 2002; Sánchez-Villagra 2010; Nengo *et al.* 2017). Although these specimens are unfortunately rare, they offer opportunities to test homology hypotheses

proposed from adult morphology (Braga 1998; Leigh 2007; Kuykendall 2019). In hominins, ontogenetic studies of the upper jaw indicate a close evolutionary relationship between *Homo* sp. and *P. robustus* (Braga 1998; Braga *et al.* 2023). Early *Homo* and *Australopithecus afarensis* juveniles further show that diagnostic species-level traits appear early in development (Alemseged *et al.* 2006; Braga & Moggi-Cecchi 2025). Thus far, our understanding of the ontogenetic mechanisms underlying robust hominin craniofacial morphology predominantly relies on infant specimens of *P. robustus* (Bromage 1989; Braga 1998; Braga *et al.* 2023). The rarity of juvenile specimens of *P. boisei* has contributed to the extrapolation of its developmental trajectories through parsimonious evolutionary scenarios (Kuykendall 2019).

Recent fieldwork conducted by the Omo Group Research Expedition (OGRE) in the Shungura formation in Ethiopia (Boisserie *et al.* 2008) has yielded new hominins fossil

evidence from the Plio-Pleistocene, offering fresh insights into the taxon's diversity and paleobiology (Daver *et al.* 2018; Delagnes *et al.* 2023; Towle *et al.* 2025; Hlusko *et al.* in press). Among those discoveries is a specimen of *P. boisei* preserving the right half of the palate of an immature individual. The objective of this study is to describe and analyze this juvenile specimen of *P. boisei*. Our analysis of this fossil has three aims: 1) determine the relative developmental stage of this individual compared to other known infants of *Paranthropus*; 2) shed light on the craniofacial ontogeny of *P. boisei*; and 3) test the hypothesis of a shared facial ontogenetic pattern with *P. robustus*.

MATERIAL

DISCOVERY AND GEOLOGICAL CONTEXT

OMO 362-10001 was discovered by Alemayehu Asfaw on July 17th, 2012, on a small outcrop of the Errum sector in the southern extension of the Shungura Formation (so-called “Kalam area”) at 4°84'8N, 35°94'5E. This discovery was made during lunch break, which A. Asfaw often partially skipped for extra survey time. We mention these circumstances here to remind the decisive contribution of African fossil collectors to the collective effort of building the African fossil record, through their hard work and, often, with passion. This is definitely the case with Alemayehu Asfaw, to whom we would like to pay an enthusiastic tribute for his love of human deep history and for his long field paleoanthropology career, initiated in the Shungura Formation in 1973, and who was still collecting fossils with the OGRE in 2024. OMO 362 is a locality defined by the OGRE in 2012. It includes International Omo Research Expedition (IORE) locality F 412 and the type section of Member K realized by the IORE geologists in the 1970s (Heinzelin 1983). OMO 362-10001 was located about 400 m south of this section, and stratigraphic continuity can be observed between the hominin specimen outcrop and the section location. The fossil was partially buried in the altered external layer of a silty horizon attributed to Unit K-1. It was stratigraphically located 1.5 m below Tuff K-2-1, and about 5 m above Tuff K. This latter marker was radiochronologically dated to 1.526 ± 0.015 Ma by McDougall *et al.* (2012). McDougall & Brown (2006) established a tuff correlation between a vitric tuff embedded in Unit K-1 and the Tuff Koobi Fora from the eponym formation in Kenya, suggesting that the OMO 362-10001 would be *c.* 1.485 ± 0.014 Ma in age. This specimen is one of the geologically youngest specimens of *Paranthropus boisei* recorded in the Shungura Formation. OMO 362-10001 is curated at the Department of Paleontology and Paleoanthropology of the Ethiopian Heritage Authority (EHA), Addis Ababa.

PRESERVATION

OMO 362-10001 (Fig. 1) is a right hemi-maxilla fragment exhibiting erupted dP^3 (eroded lingual fragment), dP^4 , and M^1 , and including the unerupted canine, P^3 and P^4 (see below). A large part of the premaxilla is missing mesial of

the dP^3 . The buccal root of the dP^3 , half of the permanent P^3 , and permanent canine crowns are exposed, the latter two located in their respective crypts. The zygomatic process is represented only by its root. The anterior chamber of the maxillary sinus floor is well preserved, along with a part of the right side of the nasal floor. The preserved palate extends from the mesial aspect of the dP^3 to the distal part of the M^1 and extends medially to the presumed intermaxillary suture. On the lateral side, the alveolar process shows weathering and fragmentation. Distal fracture of the maxilla exposes the buccodistal root of the M^1 .

COMPARATIVE DATA AND MATERIAL

We compared the OMO 362-10001 permanent and deciduous dentition to data culled from the published literature for a comparative sample of African Plio-Pleistocene hominins (Appendices 1; 2). Additionally, we compared the maxilla of OMO 362-10001 to high-resolution casts of adult *P. boisei* specimens housed in the Dental Anthropology Laboratory at CENIEH. The examined specimens include OH 5, KNM-WT 17400, KNM-ER 732, KNM-ER 406, KNM-ER 405, KNM-CH 1b, and OMO 323-1976-896. Additional comparisons were conducted using the digital 3D model of OH 5 (*P. boisei*; Tobias 1967; accessed via Morphosource, Media ID: 000005731) and the recently published *P. robustus* infant KW 9000 (Braga *et al.* 2023; available on Dryad: <https://doi.org/10.5061/dryad.flvhhmh22>). We further incorporated comparative data from the literature, drawing on published descriptions, measurements, and qualitative assessments of *P. boisei* and other Plio-Pleistocene hominins.

In this study, we assume that the adult morphology of *P. boisei* in our sample represents the phenotype that OMO 362-10001 could have potentially developed had it reached adulthood.

METHODS

OVERVIEW

The study of OMO 362-10001 comprises three parts. We first analysed the permanent dentition, providing a taxonomic attribution for the specimen. This involves comparing the metrics and anatomy of its permanent teeth with a sample of African Pleistocene hominins. We then estimated the specimen's ontogenetic age at death by comparing the mineralization stages of its permanent and deciduous teeth with a sample of previously described juvenile *P. robustus* and *P. boisei* (Dean 1987; Smith *et al.* 2015b; Braga *et al.* 2023; Braga & Mogggi-Cecchi 2025). After investigating the morphology of the deciduous dentition, we finally analyzed the morphology of the hemimaxilla. The latter two sections provide insights into the specimen's ontogeny and juvenile-related paleobiology, through metric and non-metric comparisons with adult and juvenile hominins. The manuscript is structured following these analytical steps. Data for these analyses were collected from the 3D model print replica of the fossil and from the virtual 3D volume of the specimen (Microtomograph Easycom, platform platina, university of Poitiers).

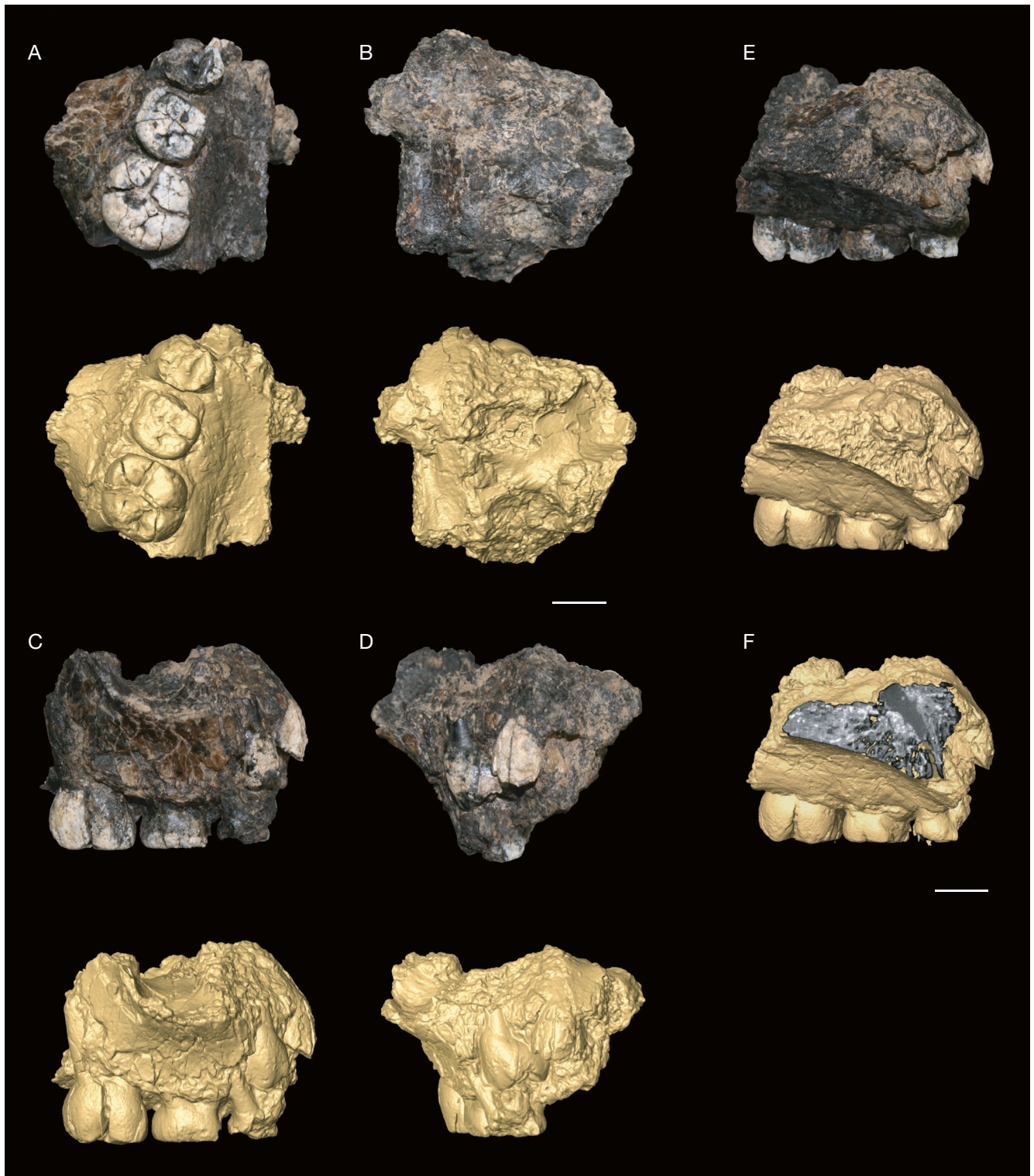


FIG. 1. — Photographs of the original OMO 362-10001 fragmentary right hemi-maxilla fossil and the corresponding microCT-based external surface reconstruction: A, palatal view; B, dorsal view; C, lateral view; D, rostral view; E, medial view; F, medial view of the subnasal morphology through Ct-scans. Scale bars: 10 mm. Credits: The authors.

PERMANENT DENTITION

Morphology and preservation

Permanent premolars and canines were virtually extracted from their respective crypts using segmentation and 3D volume

reconstruction on Avizo (enamel and dentine were segmented separately). Physical casts were then generated from these 3D reconstructions. These isolated volumes and casts were used for the analysis detailed below (Appendices 3; 4).

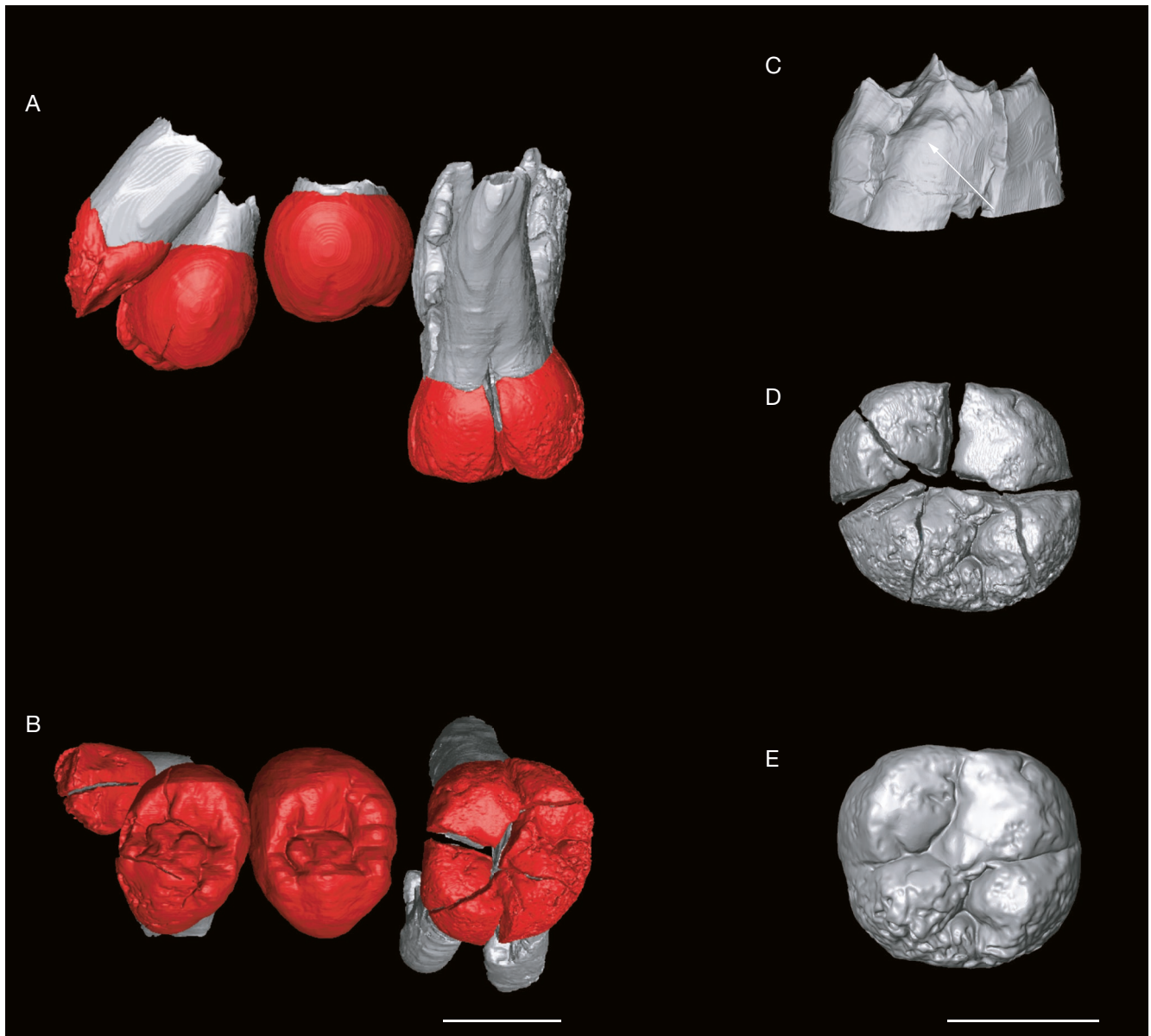


FIG. 2. — OMO 362-10001: **A**, **B**, lingual (**A**) and occlusal (**B**) view of the permanent dentition; **C**, mesiolingual view of first molar enamel-dentine junction (EDJ), with **white arrow** indicating Carabelli feature (see text); **D**, occlusal view of the original fragmented first molar; **E**, occlusal view of the restored first molar. Scale bars: 10 mm. Credits: The authors.

Each tooth was described to provide a detailed overview of the state of preservation, crown morphology, and the presence and expression of morphological traits. The level of tooth wear is quantified following Scott (1979)'s scoring system. The anatomical nomenclature follows standard practice (e.g., Turner *et al.* 1991; Wood 1991). Anatomical comparisons were made with individuals belonging to early *Homo*, *P. robustus*, and *P. boisei* (Appendix 1).

Linear metrics

The maximum mesiodistal (MD) and buccolingual (BL, for post-canine teeth) or labiolingual (LL, for canine tooth) dimensions of the permanent tooth crowns of specimen OMO 362-10001 were measured using a digital caliper from

the cast replica, following Tobias (1967) and Wood (1991). Two measurements of each dimension were provided for the first molar: one obtained directly from the fragmented tooth, and another from the 3D digital tooth reconstruction in Avizo (Fig. 2D, E). Only labiolingual breadth is available for the canine due to the infeasibility of crown reconstruction. The obtained values for OMO 362-10001 were compared to those of individuals belonging to early *Homo*, *P. robustus*, and *P. boisei* from the literature (Appendix 2).

Enamel thickness

2D enamel thickness measurements of the permanent dentition of OMO 362-10001 were collected from a digital model of each tooth, following Benazzi *et al.* (2014) guidelines.

A digital cross-section perpendicular to the cervical plane and passing through the cusp tip of the paracone and protocone of the tooth was created on Geomagic Wrap software (version 2024.0.0, 3D Systems, Rock Hill). On each 2D section, three variables were measured following Martin (1985), including: area of enamel cap (mm²); area of the coronal dentine (mm²), and length of the enamel-dentine junction (EDJ, in mm). Then, 2D enamel average thickness (AET) and 2D relative enamel thickness (will be referred in the text as RET only) were computed following classical methods (Martin 1985; Lockey *et al.* 2020) as follows:

AET = area of enamel cap / EDJ length

RET = (AET / sqrt(area of dentine)) × 100

Due to the fragmented nature of the first molar, a correction was made following Smith *et al.* (2003), where gaps between the tooth fragments are subtracted from the total measurements.

DETERMINATION OF RELATIVE AGE AT DEATH

We recorded the mineralization stage of the deciduous and permanent teeth of OMO 362-10001 using a scale with 14 successive stages indicating the proportion of crown and root formed, following Moorrees *et al.* (1963). Recent studies have used Moorrees *et al.* (1963)'s scale to document the tooth mineralization stages of infant specimens in *Paranthropus robustus* and *P. boisei* (Braga *et al.* 2023; Braga & Moggi-Cecchi 2025), whose ages at death were previously determined through histological methods (Dean 1987; Smith *et al.* 2015b). Comparison with infants of *P. robustus* was necessary because of the limited sample of juvenile specimens of *P. boisei* (Kuykendall 2019). By comparing the developmental stage of OMO 362-10001 with these southern and eastern African specimens, we estimated the Omo specimen's relative age at death.

The 14 stages provided by Moorrees *et al.* (1963) and used as in Braga *et al.* (2023), indicate the proportion of crown (Cr) and root (R) complete or resorbed: 0, no sign of crypt formation; 1, empty crypt; Cr i, crown initiated; Cco, cusps coalescence; Cr oc, crown outline complete; Cr 1/2, crown 1/2; Cr 3/4, crown 3/4; Crc, crown complete; Ri, root initiated; Cli, cleft initiated; R 1/4, root 1/4; R 1/2, root 1/2; R 3/4, root 3/4; Rc, root complete; A, apex 1/2; and Ac, apex complete.

DECIDUOUS DENTITION

Following the same methods as for permanent dentition, deciduous premolars were described (i.e., morphological traits, wear pattern) and MD-LL measurements obtained. The linear dimension could only be measured (LL) or estimated (MD) for the dP⁴ due to the fragmentary nature of the dP³. For the dP⁴, the mesiodistal width was estimated due to the fragmented nature (missing enamel) of the mesial aspect of the crown. This estimate represents the mean value between the minimum value, which is the fragmented crown dimension, and the maximum value, which is the dimensions at contact with the dP³. These dental dimensions for OMO 362-10001 were compared to the statistical summaries of various Plio-Pleistocene hominin species provided by Bailey *et al.* in 2019, including *A. africanus*, *A. afarensis*, *P. robustus*, *P. boisei*, and early *Homo*.

MAXILLARY MORPHOLOGY

The right hemimaxilla was reconstructed from 50-μm CT data and used to digitally reconstitute the left side by mirror-imaging in Avizo (version 2024.2, Thermo Fisher Scientific). From this bilateral reconstitution, we estimated depth and breadth measurements of the palate. OMO 362-10001 is fractured sagittally along the maxillary suture, evidenced by the presence of interdigitation structures, incisive foramen along the break, as well as the maxillary-vomer crest. Therefore, we were confident in applying a mirror reconstitution of the preserved side (Figs 1; 3). The vault angle of the palate was determined based on the occlusal wear plane of the dentition.

The maxillary bone anatomy of OMO 362-10001 was described from several perspectives, following previous studies (Kimbel *et al.* 1997; Clarke 2012; Braga *et al.* 2023). The palatal morphology (i.e., palate breadth and palate depth) was measured on the reconstructed maxilla (Fig. 3). Palate breadth was measured as the internal distance between the alveolar process taken at the dP³, dP⁴ and M¹ level for OMO 362-10001, and P³, P⁴ and M¹ for OH 5. Palate depth was measured following Wood (1991): as the height in the midline of an imaginary line joining the alveolar process and the roof of the palate. Palate depth measurements were taken at the dP³, dP⁴ and M¹ level for OMO 362-10001 and P³, P⁴ and M¹ for OH 5. We studied OMO 362-10001 subnasal morphology using direct examination of medial slice through the midline of the hemi-maxilla using CT scans of the specimens. Hard palate thickness was measured as the vertical palate dimension, immediately posterior to the incisive canal upper aperture, just off the midline following McCollum *et al.* (1993). All measurements were made using Avizo and ImageJ (version 1.54m).

ABBREVIATIONS

AET	average enamel thickness;
BL	buccolingual;
DMR	distal marginal ridge;
EDJ	enamel dentine junction;
EHA	Ethiopian Heritage Authority;
IORE	International Omo Research Expedition;
LL	labiolingual;
MD	mesiodistal;
MMR	mesial marginal ridge ;
OGRE	Omo Group Research Expedition;
RET	relative enamel thickness;
y.o.	years old.

RESULTS

PERMANENT DENTITION

Description (Fig. 2A, B; Appendices 3; 4)

Canine. Right C (3D reconstruction from CT scans). This is a fractured postmortem permanent tooth with the apical portion missing. A significant portion of the enamel is damaged on the labial aspect. A vertical fracture divides the mesial and distal parts of the crown, extending the full length of the labial wall into the root and stopping 3 mm

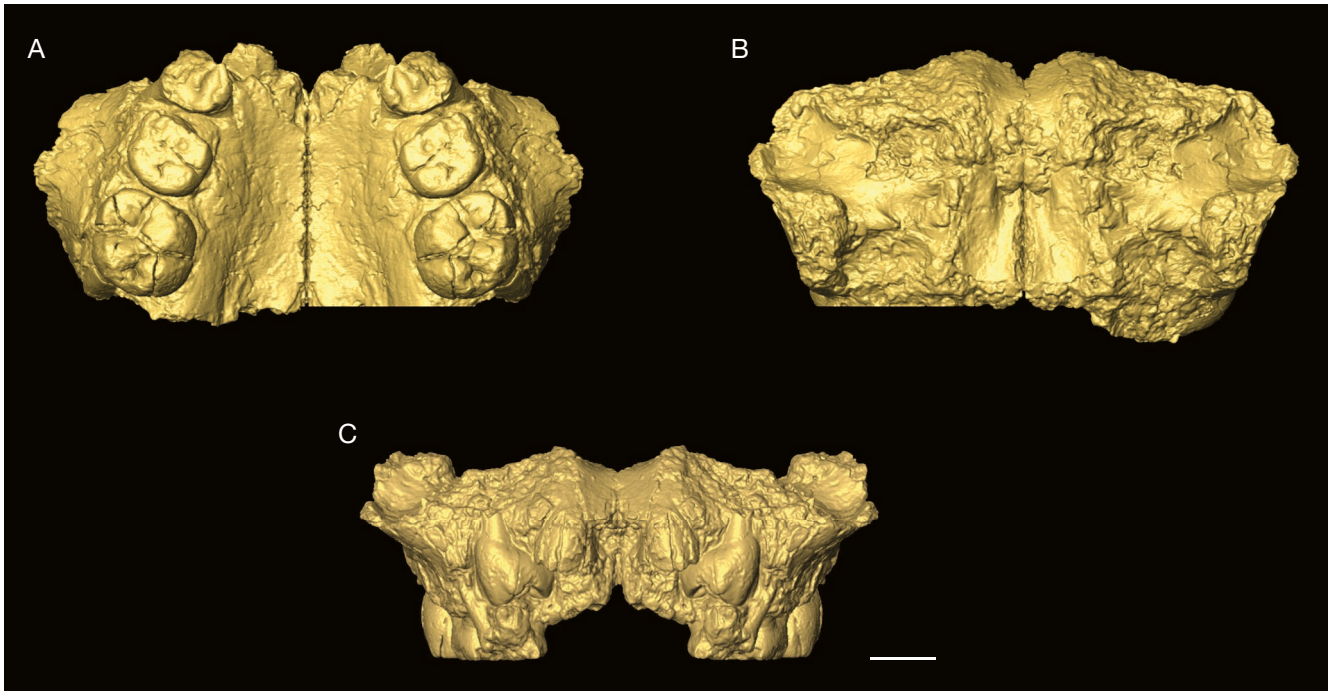


FIG. 3. — OMO 362-10001: **A**, 3D reconstitution palatal view (see text); **B**, 3D reconstitution dorsal view; **C**, 3D reconstitution rostral view. Scale bar: 10 mm. Credits: The authors.

above the cingulum on the lingual wall. In the lingual view, the crown is asymmetric, mainly due to the presence of a moderately thick MMR. The cingulum is both broad and low, extending towards the apex through a large ridge. We observe both mesial and distal fossae on each side of this ridge. The mesial ridge is narrower than the distal one. In distal view, the labial face appears more convex than the lingual one. In the occlusal view, the DMR causes a tapering of the occlusal outline distally. The root is partially developed and measures 8 mm from the cervix. It is thick and robust, mesiodistally compressed in section, and exhibits a slight distal inclination along its length.

Third premolar. Right P³ (3D reconstruction from CT scans). This is a crown germ still within its alveolar crypt. The buccal and mesial surfaces are exposed due to the fragmentary nature of the maxillary bone. The contour of this tooth is oblong, and compressed mesiodistally. The occlusal basin features a marked mesiodistal fissure, shifted lingually. Two deep buccal fissures are evident. In the lingual region, the protocone is a large cusp of the same height as the larger paracone. The pre- and postprotocrista extend mesially and distally, contributing to thick mesial and distal marginal ridges, both exhibiting accessory cusplets. In the buccal region, the endoparacrista extends lingually and is interrupted by the mesiodistal fissure; this crest appears bifurcated. The root is in the earliest stage of mineralization, measuring only 3 mm at its greatest developed length. A deep and broad mesial longitudinal groove originating at the cervix indicates the initiation of two bifurcating roots, with the buccal one larger in section than the lingual.

Fourth premolar. Right P⁴ (3D reconstruction from CT scans). This is the germ of a crown still within its alveolar crypt. The overall morphology of the crown is oblong, compressed mesiodistally. The paracone is relatively larger than the lingual cusp. The occlusal basin exhibits an angular outline in its buccal portion. The deep occlusal fissures display a distinct, asymmetric H pattern. The protocone is mesially placed relative to the paracone. The endoprotocrista is wide and interrupted by the mesiodistal fissure. The distal fissure includes a wide and deep distolingual pit as it merges with the mesiodistal groove. The DMR, of the same height as the MMR, features five accessory cusplets, with the most buccal one being the most developed, forming a distinct cusp (buccodistal cusp). In distal view, the crown's bulging aspect results in a constriction at the cervix.

First molar. This is a complete, erupted crown damaged by postmortem fractures. There are cracks between the mesial and distal cusps and between the protocone and paracone, resulting in significant tooth disjunction. The fragmentation observed on the hypocone and paracone, although narrower, also add to the disjunction of the tooth. The crown is moderately worn (grade 12, Scott 1979), with only the apex of the cusps worn flat in the following order: Protocone > Paracone > Hypocone > Metacone. This tooth has four low and bulbous main cusps bounded by deep grooves running on the occlusal surface. The crown outline is sub-rectangular in occlusal view and slightly enlarged buccolingually at the cervix. The distal contour is rounded, while the mesial edge is straighter, although no contact facets appear with the dP⁴. The paracone has

TABLE 1. — Linear dimensions of the permanent dentition of OMO 362-1001 and a comparative sample. Values are rounded for readability, except for the restored first molar of OMO 362-1001. Actual measurement values are provided in the Supplementary Data (Appendix 2). **Brackets** indicate the dimensions of the restored first molar (see text). Abbreviations: **C**, canine; **BL**, bucco lingual; **LL**, labio lingual; **MD**, mesio distal.

		C	P ³		P ⁴		M ¹	
Specimen/taxon		LL	MD	BL	MD	BL	MD	BL
OMO 362-10001		8.3	10.6	14.4	12.7	16.9	14.7 (14.16)	15.5 (14.7)
<i>Paranthropus robustus</i>	x	9.8	9.6	13.8	10.3	14.7	13.5	14.5
	min	8.8	7.7	12.8	9.5	13.6	11.6	13.6
	max	10.9	10.5	15	11	15.6	15.1	15.2
	var	0.7	0.9	0.6	0.3	0.7	1.0	0.3
	n	5	6	6	5	5	11	11
<i>Paranthropus boisei</i>	x	9.0	10.9	15.4	11.6	16.4	14.7	16.3
	min	8.2	10.2	13.9	10.5	15.2	13.6	14.9
	max	9.9	12	17	12.1	17.8	15.6	17.7
	var	0.5	0.3	1.2	0.3	1.2	0.5	0.8
	n	5	7	7	5	5	8	8
<i>Homo erectus</i>	x	11.4	8.2	11.5	8.0	11.6	12.1	13.1
	min	11.4	7.1	9.9	7	10.2	10.8	12
	max	11.4	9.1	12.8	9.2	12.7	13.6	14.5
	var	–	0.3	0.8	0.3	0.7	0.5	0.5
	n	1	17	17	14	14	17	17
<i>Homo habilis</i>	x	9.9	9.0	12.1	9.2	12.1	13.0	13.0
	min	8.5	8.1	11.1	8.6	11	11.2	11.9
	max	11.8	10.5	13.6	10.7	13.7	14.7	14.2
	var	1.5	0.5	0.5	0.5	0.8	0.6	0.5
	n	5	11	11	10	10	15	15

a mesio-buccal projection. The *crista obliqua* is thick but interrupted by a fissure at the base of the metacone (grade 2, Wood & Engleman 1988). A slight vertical groove on the mesiolingual wall of the protocone indicates the presence of a Carabelli structure (grade 1, ASUDAS) visible at the enamel-dentin junction. An inflated and low endoparacrista can be identified running lingually. The distal extension of the lingual grooves runs along the lingual side of the *crista obliqua* and isolates the hypocone, then bifurcates distally to delimit a distoconule, C5 (grade 3, ASUDAS). The distal fovea appears as a distal pit. The tooth exhibits three well-developed roots: two buccal roots, fused near the crown, and a single lingual root. All apices are open. The lingual root is thick, conical, and ovoid in cross-section with slight buccolingual constriction. It is strongly inclined lingually and slightly distally, diverging markedly from the buccal pair. A broad, shallow buccal groove suggests a double radicular canal.

The buccal roots are thinner, shorter, and mesiodistally compressed, both showing a distal inclination. A broad, shallow mesial groove on the distal buccal root indicates a possible double canal.

Morphological comparisons

The permanent dentition of this individual exhibits affinities with Plio-Pleistocene robust hominins. The presence of additional occlusal structures at the M¹, such as a distoconule (C5) or a Carabelli's trait, is a condition frequently observed in the literature for the genus *Paranthropus* (Wood & Engleman 1988) as in the comparative sample (e.g., KNM-WT 17400, KNM-CH 1B, OMO 323-1976-896,

L 50-2, DNH 39, KB 5063). Furthermore, the “inflated” aspect of the occlusal morphology (e.g., paracone endocristae, *crista obliqua*), as well as more subtle features such as a distal pit, quadrangular contours, and bulbous and low cusps morphology further reinforce the similarities between OMO 362-10001 and the robust hominins, distinguishing it from the contemporaneous early representatives of the genus *Homo*.

The fourth and third premolars also exhibit an overall morphology associated with robust hominins (Robinson 1956; Wood & Engleman 1988; Suwa 1990), including developed occlusal crests and a well-developed distal aspect of the crown. The presence of additional cusps on a strongly developed DMR described here is a common feature in specimens of *P. boisei* (Tobias 1967; Suwa 1990; Wood 1991; e.g., KNM-WT 17400, KNM-CH 1b, OH 30, L 338x-34) and in some *P. robustus* (e.g., SK 24, DNH 78, DNH 59; Robinson 1956; Moggi-Cecchi *et al.* 2010). Similarly, other characteristics present on both P⁴ and P³ further support affinity with *P. boisei*: enlarged buccal cusp relative to the lingual one, deep and continuous mesiodistal fissure (KNM-WT 17400, OH 5, OH 30; Suwa 1990).

Concerning the canine, its fragmented nature reduces the potential for morphological comparisons. However, the asymmetrical aspect of the crown in lingual view can be often observed among specimens of *P. boisei* (e.g., KNM-ER 816, KNM-ER 802, OH 5, KNM-CH1b; Tobias 1967; Leakey 1973; Leakey & Walker 1988; Wood 1991). Furthermore, some of these specimens also exhibit a developed cingulum, which is less frequent in the specimens of early *Homo* (e.g., OH 16, KNM-ER 1805, KNM-ER 1590).

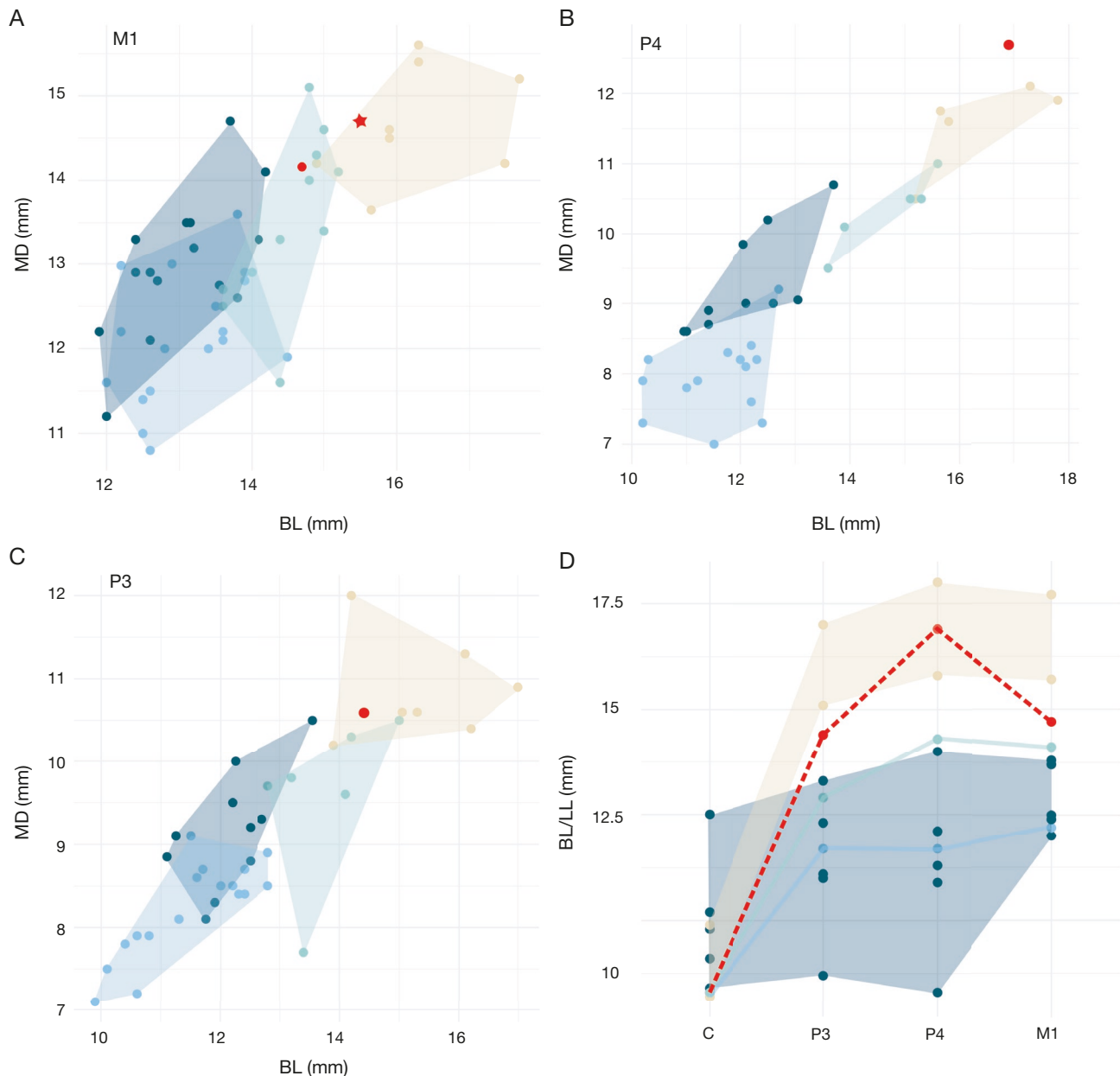


FIG. 4. — Linear dimensions of the OMO 362-10001 permanent dentition in relation to Pleistocene hominins: **A**, first molar (the red star and red points correspond to the original and restored first molar (M¹) of OMO 362-10001, respectively); **B**, permanent fourth premolar (P⁴); **C**, permanent third premolar (P³); **D**, buccolingual/labiolingual dimensions from canine to first molar. Colors: red, OMO 362-10001; dark blue, *Homo habilis*; light blue, *H. erectus*; green, *Paranthropus robustus*; light brown, *P. boisei*. Credits: The authors.

Linear metrics

Table 1 and Figure 4 present the results for the linear measurements of OMO 362-10001 and the comparative sample for the permanent dentition. The canine of OMO 362-10001 has a LL value of 8.3 mm. This measurement falls within the lower end of the range observed for *P. boisei* and below the range observed for *H. habilis*. Concerning the third premolar, with dimensions of MD = 10.6 mm and LL = 14.4 mm, both values fall within the range of variability observed in *P. boisei* while LL value also falls within the observed range for *P. robustus*. The fourth premolar has a LL measurement (16.9 mm) within the range of variability of *P. boisei*, above

species ranges of both *P. robustus* and *Homo*. The large MD value of OMO 362-10001 P⁴ exceeds the range observed for all taxa in our comparative sample but is closest to the values observed for *P. boisei*. MD dimension of the M¹ of OMO 362-10001 is 14.7 mm and the estimated LL dimension is 15.5 mm. After digital 3D reconstruction, the MD and LL dimensions are 14.2 mm and 14.7 mm, respectively. The latter MD dimensions fall within the min-max range of *P. boisei* and *P. robustus* as well as *H. habilis*. However, the corrected LL dimension falls only within the variation of *P. robustus*, below that of *P. boisei*. The LL values of OMO 362-10001 from the canine through the M¹ conform

TABLE 2. — OMO 362-10001 enamel measurements and a comparative sample from Lockey *et al.* 2020. Abbreviations: **AET**, average enamel thickness; **EDJ**, enamel-dentine junction; **RET**, relative enamel thickness.

Taxon/specimen		Enamel area (mm ²)	Dentine area (mm ²)	EDJ length (mm)	AET (mm)	RET
OMO 362-10001		53.1	56.6	20.4	2.5	34.4
<i>Paranthropus robustus</i>	x	41.3	56.2	23.6	1.8	23.4
	min	33.6	43.0	20.9	1.6	19.6
	max	51.2	67.7	27.0	2.1	27.6
	sd	7.8	10	2.3	0.2	2.8
	n	6	6	6	6	6
<i>Paranthropus boisei</i>	x	46.9	57.6	22.0	2.1	28.3
	min	36.7	47.1	20.7	1.6	21.4
	max	54.9	64.9	23.3	2.3	34.3
	sd	9.3	9.3	1.3	0.4	6.5
	n	3	3	3	3	3
<i>Homo</i> sp.	x	36.2	46.4	21.7	1.7	25
	min	30.0	37.8	20.2	1.2	16.9
	max	40.7	55.9	23.7	1.9	28.7
	sd	5	7.5	1.5	0.3	5.5
	n	4	4	4	4	4

TABLE 3. — Dental developmental stages of OMO 362-10001 and a comparative sample of *Paranthropus*, based on Moorrees *et al.* (1963) scale. Age at death are provided by Dean (1987) and Smith *et al.* (2015b). DNH 47, DNH 44, DNH 84, SK 62 developmental stages are from Braga *et al.* (2023); KNM-ER 1477 and KNM-ER 1820 developmental stages are from Braga & Moggi-Cecchi (2025). OMO 362-10001, KW 9000, and DNH 108 developmental stages were acquired by the authors. *, indicates estimated age, see text; 1, emerged M¹; 0, M¹ not emerged.

Specimen inventory	Species	dP ³	dP ⁴	C	P ³	P ⁴	M ¹	Emerged M ¹	Age at death
Maxillas									
DNH 47	<i>P. robustus</i>	R ½ - ¾	—	Cr i - ½	—	—	Cr ½	0	0.67 – 0.77
DNH 84	<i>P. robustus</i>	—	—	—	Cr oc - ½	Cr oc	Ri	0	2.24
DNH 108	<i>P. robustus</i>	—	—	R ½ - ¾	R ¼	Cli	A ½	1	5.35 – 5.53
KW 9000	<i>P. robustus</i>	Rc	R ¾ - c	Cr ½	Cr i - oc	Cr i	Ri	0	—
OMO 362-10001	<i>P. boisei</i>	Rc	Rc	R ½	R ¼	Cli	R ¾ - c	1	3.8 – 5*
Mandibles									
DNH 44	<i>P. robustus</i>	—	—	Cr ½	—	—	Cr ½ - ¾	0	1.7
KNM-ER 1477	<i>P. boisei</i>	—	—	Cr ¾	Cr ½	Cr ½	Cr c	0	2.5 – 3
KNM-ER 1820	<i>P. boisei</i>	—	—	Cr ¾ - c	Cr ¾ - c	na	Ri	0	2.5 – 3.1
SK 62	<i>P. robustus</i>	—	—	Ri	Ri	Cr ½ - ¾	Ri - ½	0	3,12

to the pattern seen in *Paranthropus*, with reduced canine size vs enlargement of the premolar and molar dimensions. For every tooth position, OMO 362-10001 is outside the range of variation observed for the genus *Homo*.

Enamel thickness

Table 2 presents the enamel thickness measurements for the OMO 362-10001 first molar. The OMO 362-10001 value of M¹ RET is 34.4 which falls just above the range of *P. boisei*. This value of RET contrasts with the variation of *Homo* sp. or *P. robustus*, falling far above them. Also, OMO 362-10001 AET value is 2.6, above the variation range of *P. boisei*, with an enamel area of 53.1 mm² falling within the variation range of *P. boisei*.

RELATIVE AGE AT DEATH DETERMINATION

Table 3 presents the developmental stage of the deciduous and permanent dentition of OMO 362-10001 alongside the comparative sample. In OMO 362-10001, the first molar is erupted and in occlusion (i.e., presence of wear facet) while

permanent canine and premolars are unerupted (Fig. 5A, B, D), though their crowns are fully mineralized (Crc), supported by initiated root development. Roots of the latter are developing (P³: Ri ¼) or at the initial stage (P⁴: Cli) while that of the canine is half complete (R ½) (Fig. 2; Appendices 3; 4). This advanced developmental stage of the permanent dentition contrasts with most of the known juveniles of *P. robustus* in which permanent canine and premolars crowns are in the forming stage and first molars have not erupted yet (e.g., DNH 47, DNH 44, DNH 84, and KW 9000; Braga *et al.* 2023). The deciduous dentition of OMO 362-10001 also shows an advanced stage of development with crown and root complete for dP⁴, where the root of dP³ has already been partially resorbed (Fig. 2; Appendices 3; 4). This advanced developmental stage is consistent with their heavy wear, indicating prolonged occlusion.

Regarding roots and crown formation, OMO 362-10001 appears significantly older than DNH 47, DNH 44 (mandible), and DNH 84 whose ages at death are respectively, 0.67-0.77 y.o., 1.7 y.o., and 2.24 y.o. (Smith *et al.* 2015b).

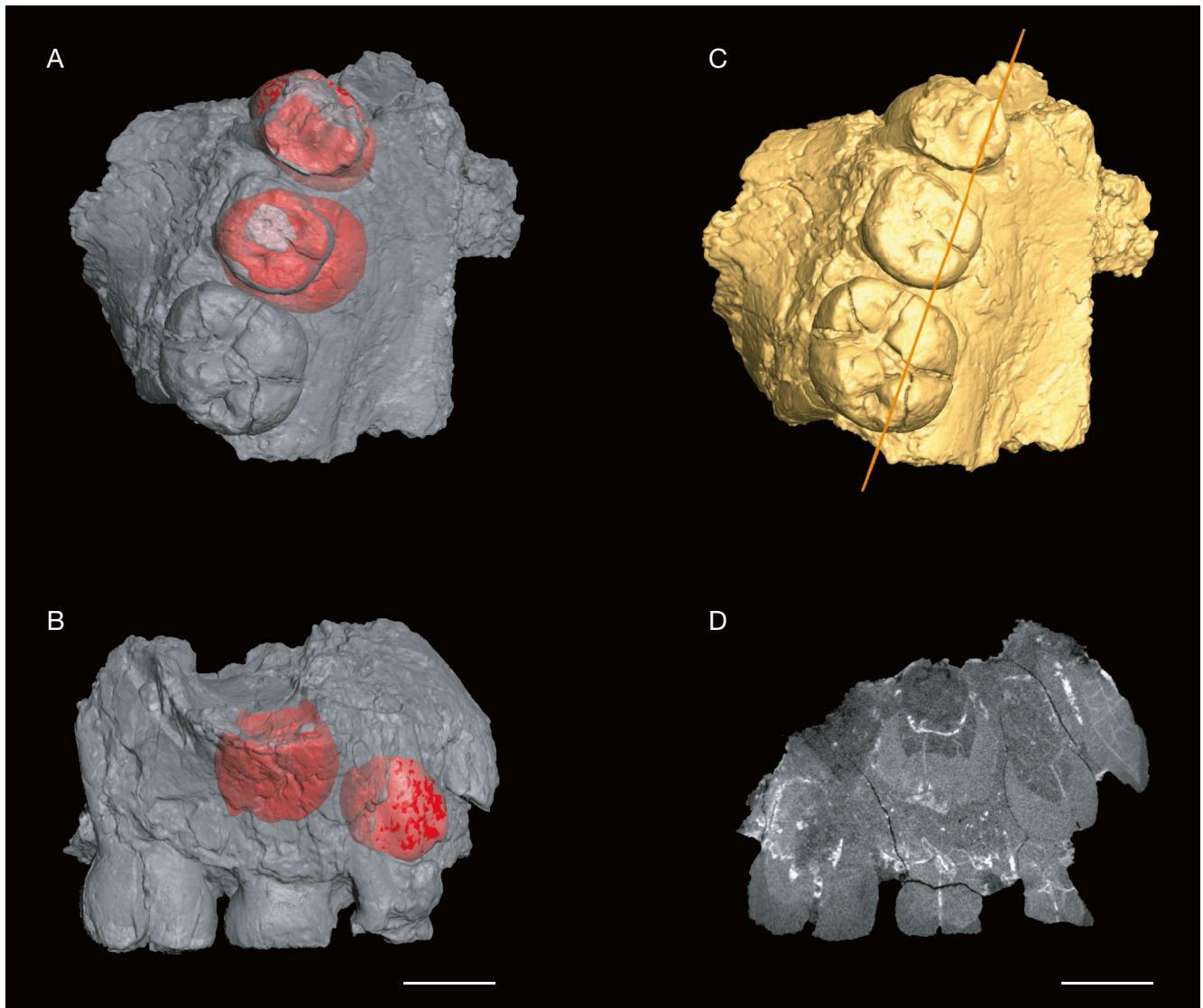


FIG. 5. — OMO 362-10001: **A**, transparent palatal view showing crowns of permanent fourth and third premolar in red. The superimposition of deciduous and permanent premolars with transparency allows to observe the discrepancy of size between them (see text); **B**, transparent lateral view with crowns of permanent fourth and third premolar in red (this view allows to observe that the third permanent premolar is closer to erupt than the fourth permanent premolar); **C**, **D**, cross section of the tooth row (**C**, orange line) and its CT-scans view (**D**). Scale bars: 10 mm. Credits: The authors.

In DNH 44 and DNH 47, the M¹ and canine crowns remain in the mineralization stage, whereas in OMO 362-10001, these crowns are fully formed with root growth initiated. The older individual, DNH 84 (2.24 y.o.), exhibits M¹ roots in the early stages of mineralization, while those in OMO 362-10001 are approaching full development. Additionally, DNH 84 shows incomplete premolar crowns, in contrast to the fully developed premolar crowns in OMO 362-10001. Also, none of those infants of *P. robustus* shows erupted M¹. Concerning specimens KNM-ER 1477 and KNM-ER 1820 attributed to *P. boisei*, estimated to be between 2.5 and 3.1 years old (Dean 1987), the crown of the former is not fully mineralized, while the root development has only just initiated in the latter. These developmental stages contrast sharply with OMO 362-10001, in which all crowns are fully mineralized, the first molar showing roots approaching

the end of formation, and both premolars and the canine displaying early root mineralization. OMO 362-10001 is therefore significantly developmentally more advanced than the other juveniles of *P. boisei* in the sample, and can be confidently considered older than 3.0 years. However, OMO 362-10001 shows a less advanced development than specimen DNH 108 attributed to *P. robustus*, as the roots of the erupted first molar are complete in DNH 108, but still-forming on OMO 362-10001. We also see a slightly more advanced development of the canine root and an erupted crown on DNH 108, but the canine is not erupted in OMO 362-10001 (Smith *et al.* 2015b; Leece *et al.* 2023). Therefore, it is unlikely that OMO 362-10001 is older than DNH 108 who has an age estimation of 5.35-5.53 y.o. (Smith *et al.* 2015b). Moreover, recent studies have attested the age of first molar eruption between 3-3.8 y.o. for *Paranthropus*

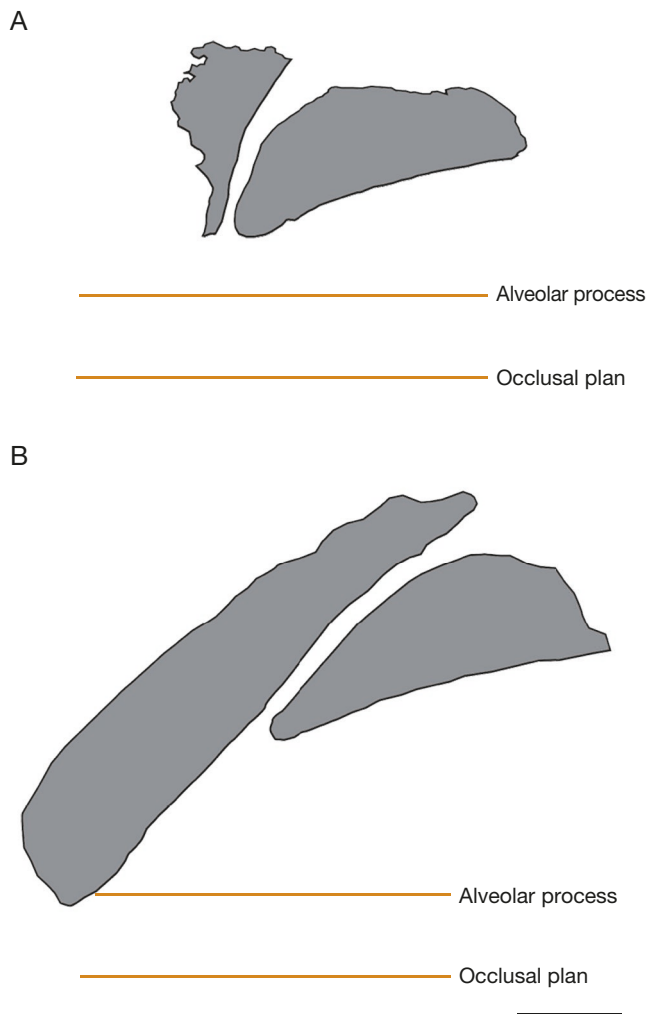


FIG. 6. — Subnasal morphology of: **A**, OMO 362-10001; **B**, OH 5. The **upper orange line** represents the average level of the alveolar process margin, while the **lower line** indicates the occlusal margin of the dentition. The premaxilla of OMO 362-10001 displays a more orthognathic configuration compared to the adult OH 5. Additionally, the level of the alveolar process highlights how much shallower the anterior palate is in OMO 362-10001 compared to the adult condition seen in OH 5. Scale bar: 10 mm. Credits: The authors.

(Kelley & Schwartz 2012; Kuykendall 2019). Given these varied results, we assigned a relative estimated age at death between 3.8-5 y.o. to OMO 362-10001.

DECIDUOUS DENTITION

Description (Fig. 1)

Upper deciduous third premolar. The tooth is fragmented, with only the lingual portion preserved, containing a large dentine exposure due to advanced wear. This elongated dentine exposure along the mesiodistal axis corresponds to remnants of the protocone and hypocone. The lingual aspect is reduced, forming a triangular outline. The roots are partially dissolved apically as the permanent P³ is in the crypt above.

Upper deciduous fourth premolar. The tooth is incomplete, with the mesial portion of the enamel cap missing. This tooth exhibits significant tabular occlusal wear (grade 19, Scott

1979). The dentine is exposed on the protocone, paracone, and metacone as follows: Paracone = Protocone > Metacone. This tooth exhibits a molariform structure with a rectangular outline, enlarged buccolingually. The mesial projection of the buccal cusps relative to the lingual cusps results in a slight asymmetry of the crown's outline in occlusal view. The hypocone is well-developed and delimited by the lingual fissure mesially and by the distal fovea in its buccal region. This distal fovea forms a pit and is delimited distally by a thick marginal ridge, bearing a distoconule. Despite the extensive wear, a developed *crista obliqua* can be observed. The protocone appears enlarged buccolingually and is separated from the hypocone by a deep and wide lingual fissure. The paracone is mesiobuccally projected. In distal view, the lingual wall is relatively straight, while the buccal wall is convex, particularly at the cervix where the crown has a “strangled” appearance. This tooth exhibits three developed and diverging roots.

Morphological comparisons

Concerning the dP³, few observations can be made based on the fragmented nature of this tooth. However, the absence of a mesiolingual corner's projection (*tuberculum molare*) corresponds to what is described as a condition of *Paranthropus* by Bailey (2017) and Leece *et al.* (2022).

The dP⁴ morphology of OMO 362-10001 conforms to the common pattern observed in Plio-Pleistocene hominins, characterized by four primary cusps with a *crista obliqua* and bulbous wall morphology. The presence of a prominent distal marginal ridge, as seen in OMO 362-10001, is a common trait in *P. robustus* (e.g., DNH 57, DNH 30, and KW 9000), as originally described by Robinson (1956). A similar feature is also evident in the OH 30 and L 144-23 teeth attributed to *P. boisei* (Tobias 1991; Brophy *et al.* 2021). This feature is less frequent or absent in early *Homo* (e.g., UW 101-1376) and *A. africanus* (e.g., Sts 24), where the distal aspect of the crown is low and incised by the buccal limb of the foveal groove (Robinson 1956). The presence of a distoconule (C5) is described as frequent in *Paranthropus* and shows the highest frequencies in *P. robustus* (Bailey 2017; Bailey *et al.* 2019). The relatively well-developed hypocone, as observed in OMO 362-10001, is a common feature in dP⁴ of *Paranthropus* compared to other hominins (Moggi-Cecchi *et al.* 2010; Leece *et al.* 2022). The dP⁴ of OMO 362-10001 exhibits no contact with the M¹, resulting in a gap, supported by the absence of interproximal wear facets. This characteristic is not present *A. africanus* juvenile specimens (e.g., Stw 160, Taung 1).

Tooth linear metrics

Mesiodistal and buccolingual measurements of the deciduous dentition of OMO 362-10001 and of the comparative sample are presented in Table 4.

BL dimension of the dP⁴ is 12.4 mm, falling within the upper range of variation observed in *A. afarensis* and *P. robustus*. However, this value exceeds those of Early *Homo* and *A. africanus* but is lower than those of *P. boisei*. Regarding MD value of the same tooth, the measurement of the incomplete crown is 11.7 mm, while the measurement at the dP³ contact point

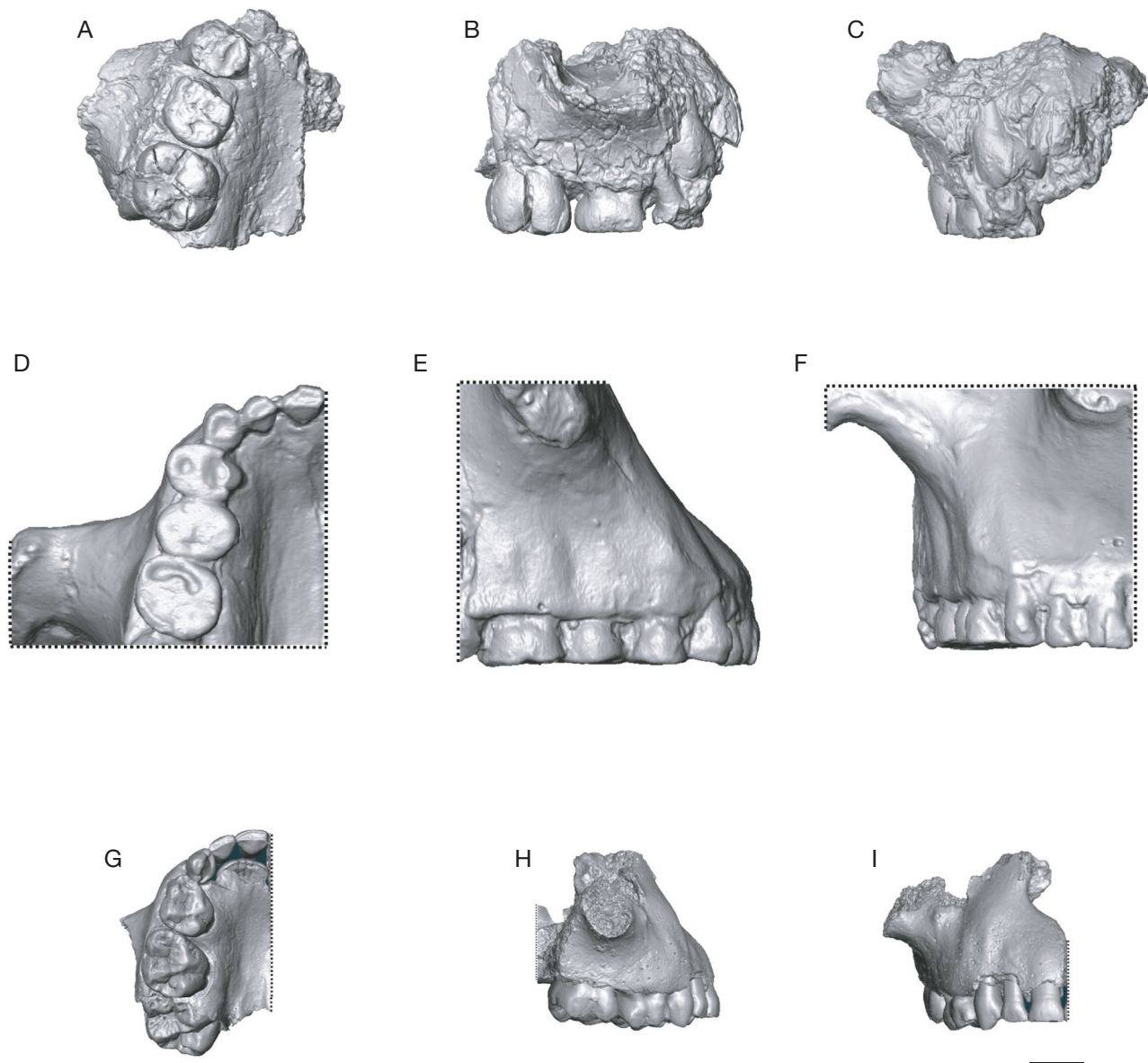


FIG. 7. — Comparative plate: **A-C**, OMO 362-10001: **A**, palatal; **B**, lateral; **C**, rostral view; **D-F**, OH 5: **D**, palatal; **E**, lateral; **F**, rostral view; **G-I**, KW 9000: **G**, palatal; **H**, lateral; **I**, rostral view. Scale bar: 10 mm. Credits: The authors.

TABLE 4. — Fourth deciduous premolar linear dimensions of OMO 362-10001 and a comparative sample from Bailey *et al.* (2019). *, estimated dimension, see text. Abbreviations: **BL**, bucco lingual; **MD**, mesio distal; **sd**, standard deviation.

Taxon/specimen	BL					MD				
	n	x	sd	min	max	n	x	sd	min	max
OMO 362-10001	1	12.4	—	—	—	1	12.4*	—	—	—
<i>Australopithecus afarensis</i>	5	11.2	0.9	10.6	12.6	4	9.9	0.1	9.8	9.9
<i>Australopithecus africanus</i>	2	11.2	—	11.0	11.4	3	10.5	0.5	9.5	11.6
<i>P. aranthropus robustus</i>	12	11.8	0.6	11.0	12.7	8	10.8	0.4	10.2	11.5
<i>P. aranthropus boisei</i>	2	13.7	—	13.1	14.3	2	13.8	—	13.1	14.6
early <i>Homo</i>	6	11.0	0.7	10.2	11.9	6	10.9	0.7	9.7	11.6

reaches 13.3 mm, therefore, the estimated value is 12.4 mm. The lowest value (11.7 mm) is slightly above the mesiodistal values of most species except for *P. boisei* which exhibits

higher MD dimensions. The mean value (12.4 mm) also falls within this range. Nonetheless, the highest value (13.3 mm) falls within the lower range of variation observed in *P. boisei*.



FIG. 8. — Comparison of the dental arch by a hypothetical occlusion between KNM-ER 1477 and OMO 362-100001. The resulting occlusion shows some consistency between the dental arches of both individuals. For the dentition, external and internal **orange circles** represent the limits of the crown and the occlusal basin, respectively. The **orange line** represents the midline along which the two jaws align. Scale bars: 10 mm. Credits: The authors.

MAXILLA

Morphology (Fig. 1)

Although a large part of the nasoalveolar clivus is missing, a small part of the floor of the nasal aperture is observed above the exposed permanent canine, represented by a steep smooth bone surface, leading posteriorly to the nasal floor of the palate. The exposed permanent canine is situated anterior to the permanent P^3 level, above it. The occlusal tip of the P^3 is in contact with the inferior part of the dp^3 , close to the occlusal margin of the alveolar process. The dp^4 and the permanent M^1 occlusal surfaces seem to be aligned in the same flat wear plan. A small gap appears between these two teeth. In the lateral aspect, the broken root of the zygomatic process extends from the body of the maxilla in a gradual and continuing slope. It extends from the distal part of the dp^3 to the mesial part of the M^1 . Its posterior border is obliquely oriented.

Medially, the hard palate is seen as a thick bone with its superior surface corresponding to the nasal floor, flat and parallel to the occlusal surface of the teeth. Sediment matrices fill the palato-nasal aperture and extend laterally, preventing direct observation of this part. The oral surface of the hard palate exhibits a gradual slope along the antero-posterior axis, leading to an increasing depth of the palate distally along the tooth row.

A midsagittal cross-section gives good insight into the sub-nasal morphology of OMO 362-10001 (Figs 1F; 6). Anteriorly, the premaxilla is set slightly obliquely and overlaps the anterior part of the hard palate. The latter tapers anteriorly and is strongly inclined showing an inferior flexion from the posterior to anterior parts, and exhibits a progressive narrowing of the posterior region behind the superior palato-nasal aperture. The latter is located at the level of mid- dp^4 . Right posterior to this palato-nasal aperture, the hard palate thickness is 9.94 mm (Table 5).

Superiorly, the maxillary sinus is divided into two main chambers, enclosed by strong walls. The anterior chamber, shallow and wide, extends laterally from the remnant of a septum to the lateral edge of the zygomatic process: the *recessus zygomaticus*. Anteriorly, the maxillary sinus extends beyond the palato-nasal canal aperture at the level of the dp^4 mesial wall in its most medial part, where its lateral part extends further, at the level of dp^3 distal wall. In the most posterior part, a small and incomplete septum that extends laterally delimits a second, deeper chamber, that falls below the nasal floor level. In its conserved lateral part, the distobuccal root of the M^1 is exposed in the cavity. In the most medial part of the hemimaxilla, the smooth nasal floor extends antero-posteriorly from the posterior edge of the palate to the level of the anterior border of the first maxillary sinus chamber. In its posteromedial aspect, the remnant of the maxillary crest, holding the absent vomer bones, extends anteriorly.

In palatal view, the alveolar process is thick mediolaterally and gradually diverges from the sagittal line of the palate. Relative to the midline, the hemi-palate appears narrow. In the posterior region, the greater palatine groove extends anteriorly to the level of the M^1 . In the anterior region, the foramen incisive can be seen as a small and elongated aperture at the level of the dp^3 . It is enclosed laterally by the remains of the premaxilla, delimited in its posterior part by a apparent suture that separates it from the palate.

Morphological comparison (Fig. 7)

Palate shape and morphology. The thick alveolar process of OMO 362-10001 is reminiscent of the morphology observed in some adult specimens of *Paranthropus* (e.g., OH 5, KNM-CH 1b, KNM-ER 405, SK 52). Palate depth substantially increases posteriorly as described in *P. robustus* and *P. boisei* (Tobias 1967; Kimbel *et al.* 2004). The estimated depth of the palate at the M^1 (11.6 mm) falls far below the variation of *P. boisei* (Table 5). The adult condition includes a deeper anterior palate, whereas OMO 362-10001 exhibits a notably shallow one (Table 5). A deep anterior palate is a distinctive trait of *P. boisei* (Rak 1983; Bromage 1989; Wood 1991). Concerning palate size, estimated internal breadth shows values lower than *P. boisei* adults, especially in the anterior part (Table 5). The relative position of the incisive foramen – aligned with the mesial part of dp^3 in OMO 362-10001 – is consistent with observations in adult *P. boisei* specimens (OH 5, KNM-ER 406, KNM-CH1b). In juvenile hominins, *P. robustus* specimen KW 9000 shows a more anteriorly placed foramen compared to OMO 362-10001. The presence of the anterior end of the great palatine groove at the M^1 level is the common condition observed in mature hominins (e.g., OH 5, SK 48, A.L. 444-1, KNM-ER 42703), where it reaches forward to the distal level of dp^4 in juveniles KW 9000 and Taung child (Wood 1991; Kimbel *et al.* 2004).

The tooth row of OMO 362-10001 is more rostrally convergent relative to the sagittal line than the more parallel conformation commonly observed in adult *Paranthropus* (Leakey & Walker 1988; Wood 1991; Rak *et al.* 2021). This difference is particularly evident in OH 5 and KNM-ER 406

TABLE 5. — Palatal measurements of OMO 362-10001, OH5 and KW 9000. All in millimeters. Last column indicates the degree of differences between OMO 362-1001 and average value of *Paranthropus boisei* adults, in mm and percentage. *, indicates measurement from Braga *et al.* (2023); **, KNM-CH1b is a half broken maxilla, measurements are estimated; ***, only OH 5 hard palate thickness value were obtained.

Features	OMO 362-10001	KW 9000	OH 5	KNM-WT 17400	KNM-ER 406	KNM-ER 405	KNM-CH1b **	<i>P. boisei</i> adult mean
Hard palate thickness	9.9	2.9*	11.2	—	—	—	—	11.2***
Palate breadth at M ¹	33.1	—	37.6	32.1	31.8	—	—	33.8
Palate breadth at dP ⁴ - P ⁴	29.1	24.1	33.5	27.5	31.5	—	—	30.8
Palate breadth at dP ³ - P ³	22.2	22.0	29.3	29.4	29.4	—	—	29.3
Palate depth at M ¹	11.6	—	19	14	17.8	19.2	17.1	17.4
Palate depth at dP ⁴ - P ⁴	5.7	7.0	12.9	9.3	11.8	15.1	13	12.4
Palate depth at dP ³ - P ³	2.2	6.9	8.72	5.5	8	9.2	7.7	7.8

and is further supported by the increasing palate breadth difference in the anterior region compared to the adult condition. However, some specimens, such as KNM-ER 405 and KNM-WT 17400, exhibit conditions more similar to OMO 362-10001. Additionally, mandibles such as Peninj-1 and OMO L7A-125 display tooth rows with a similarly oblique orientation. When superimposed in occlusion with the juvenile mandible KNM-ER 1477, the dental arcade shape is also comparable (Fig. 8).

Sub-nasal morphology (Fig. 6). OMO 362-10001 shows evidence of an inferior flexion of the palate like that of robust hominins (Kimbel *et al.* 2004). OMO 362-10001 has the usual robust morphology described by Kimbel *et al.* (2004: 181), in which “the entire palatine process of the maxilla is strongly tilted upward and backward, marking a substantial posterior increase in palate depth”. Moreover, the anteriorly tapering palate is consistent with the adult’s morphology in *Paranthropus* (Rak 1983; McCollum 1999). However, when compared to the adult OH 5 or OMO 323-1976-896, the premaxilla of OMO 362-10001 is set much more vertically than the prognathic orientation of the former (Kimbel *et al.* 2004). In OH 5, the premaxilla protrudes antero-inferiorly, positioning the alveolar process significantly below the palate, contrasting with OMO 362-10001 condition. These results echo the discrepancies in anterior palate depth between OH 5 and OMO 362-10001.

The palate of OMO 362-10001 is thick (9.94 mm), comparable to that observed in the literature for adults of *P. robustus* (mean = 9.2 mm; s = 2.2) and *P. boisei* (mean = 11.3 mm; s = 4) (McCollum *et al.* 1993). This contrasts with what is observed in the younger *P. robustus* (KW 9000, KW 10840) and *A. africanus* (Taung-1), in which the palate is thinner (2.9 mm, 2.5 mm and 3.2 mm respectively; Braga *et al.* 2023). Also, KW 9000 shows an anterior steepness of the palate less pronounced than OMO 362-10001 and adults of *P. robustus* (Braga *et al.* 2023). Zygomatic root position and morphology: The oblique posterior wall of the zygomatic root, as well as the steep inferior outline, is also similar to the adult’s condition in *P. boisei* as described by Rak (1983) with the root of the zygomatic-process thin anteroposteriorly assuming the shape of an obliquely oriented plate. This condition can be easily seen in OH 5, KNM-ER 732, KNM-ER 406, KNM-WT 17400 whereas it is less obvious in SK 52

or TM 1517 which show a straighter posterior wall and a rounded outline, as *A. afarensis* (e.g., A.L. 444-2), and juvenile KW 9000 *P. robustus* as well, which seems to be the hominin primitive conditions (Kimbel *et al.* 2004; Braga *et al.* 2023). The anteroposterior thickness of the zygomatic root appears relatively thin as OH 5, but thicker than KNM-ER 406 or KNM-ER 732, also it is substantially more developed than what is observed in KW 9000 or in juveniles of *A. africanus* and *A. afarensis* (Taung child, DIK-1-1; Tobias 1967; Wood 1991; Alemseged *et al.* 2006; Braga *et al.* 2023).

The anteriorly placed position of the zygomatic root, at the distal level of the dP³, is close to what is observed in some adult robust specimens where it is set posterior to the P³, such as in SK 52, KNM-WT 17400, KNM-ER 405, and at the P⁴ level as observed on OH5, KNM-ER 732, KNM-ER 406 and TM 1517. The condition observed in OMO 362-10001 (i.e., the anterior positioning of the zygomatic root) is also observed in the juvenile specimens of *P. robustus* (i.e., KW 9000), while the juvenile *A. africanus* (Taung child) shows more posteriorly placed zygoma roots, similar to that of adults in the same species (Braga *et al.* 2023).

In OMO 362-10001, the zygomatic arch (zygomaticoalveolar crest) slopes gradually, taking off directly from the inferior alveolar margin. This contrasts with adult *Paranthropus* specimens, where the arch originates much higher above the alveolar margin, creating a vertically expanded alveolar wall, as seen in OH 5 and SK 52. However, some variation exists, as observed in KNM-ER 406 and KNM-ER 732, where the zygomatic root takes off more gradually, though the alveolar wall remains taller than in OMO 362-10001. According to this feature, the KW 9000 individual is more comparable to the robust adult condition, showing a zygomatic process situated 6 mm above the inferior margin, although *A. africanus* Taung child also exhibit higher alveolar wall (Braga *et al.* 2023).

Dorsal morphology. The maxillary sinus morphology in OMO 362-10001 is similar to what is observed in adult *Paranthropus*. The subdivision of a large anterior chamber extending laterally into a *recessus zygomaticus*, enclosed by a thick wall and delimited posteriorly by a thin septum is clearly observed in OH 5 and DNH 7 specimens as well as KNM-ER 405, KNM-ER 733, and KNM-ER 732 (Kimbel *et al.* 1997; Kimbel *et al.* 2004; Rak *et al.* 2021). The presence of a posterior secondary deeper chamber is also consistent

with the adult morphology in *Paranthropus*. However, very minor variations exist between OMO 362-10001 and OH 5. In the former, the *recessus zygomaticus* margin reaches more anterior than the antero-medial one, where this condition is reversed in OH 5 and the DNH 7 *P. robustus* adult. This slight difference causes a more oblique orientation of the anterior chamber's lateral extension in OMO 362-10001 relative to OH 5. The presence of a maxillary crest is common in *P. boisei* specimens (Rak 1983) and is observed in OH 5 and KNM-ER 405.

DISCUSSION

TAXONOMIC ASSESSMENT OF OMO 362-10001

Morphology of the permanent dentition of OMO 362-10001 shows close affinity with *P. boisei*, exceeding the dimensions observed in *Homo* and, to a lesser extent, in *P. robustus*. The OMO 362-10001 M¹ exhibits an anatomy that matches that of *Paranthropus*, characterized by low and rounded cusps, well-developed occlusal structures, and increased occlusal complexity. The morphology of the premolars also provides significant correspondence with *Paranthropus*, with a developed distal ridge and the presence of additional occlusal structures responsible for their characteristically high dimensions and enlarged talon (Robinson 1956; Suwa 1990). Despite the lack of data regarding the anatomy of the canine of OMO 362-10001, its smaller labiolingual dimensions relative to the buccolingual dimensions of premolars and molars are characteristic of the genus *Paranthropus*. The RET value of M¹ falls within the “hyper-thick” category (RET > 25; Grine 1988) expected for a specimen of *Paranthropus*, and among the highest thickness value of *P. boisei*. The increase in enamel thickness is also a known trend in *P. boisei*, further bolstering the attribution of the Omo specimen to *P. boisei*.

AGE AT DEATH AND DENTAL DEVELOPMENT

When compared to the developmental status of known juveniles of *P. boisei*, i.e., KNM-ER 1820, KNM-ER 1477, OH 30 and KNM-ER 812, for which age at death is estimated at 2.7–3.3 y.o., 2.5–3.0 y.o., 2.7–3.2 y.o. and 2.5–3.0 y.o. respectively, OMO 362-10001 shows a more mature stage of development (Dean 1987; Beynon & Dean 1988; Kelley & Schwartz 2012). We estimate the age-at-death for OMO 362-10001 as 3.8–5 y.o., placing it among the oldest juveniles of *P. boisei*, along with L 338/y-6 (estimated at 10 ± 2 years; Rak & Howell 1978) and L 472-7, which exhibits a dental development closely resembling that of OMO 362-10001 (Beynon & Dean 1988; personal observations).

DECIDUOUS DENTITION

The attribution of OMO 362-10001 to *P. boisei*, along with its associated dP⁴, enriches the limited sample of deciduous dentition for this species. The anatomy of the dP⁴ aligns well with what is expected for *Paranthropus* and more specifically *P. boisei*, showing similarities with L 144-23 from Shungura

and OH 30 from Olduvai. However, OMO 362-10001's dP⁴ exhibits smaller overall dimensions than expected for *P. boisei*. This contrasts sharply with the incoming permanent P⁴, which is significantly larger (Fig. 5A, B, D). We therefore hypothesize that the gap between M¹ and dP⁴ provides space for the larger incoming permanent P⁴, reflecting a coordinated developmental relationship between jaw growth and tooth eruption. This echoes the hypothesis suggesting that differential regional growth rates of the mandibular corpus contribute to maintaining ontogenetic and functional compatibility between developing teeth and the surrounding bone structure (Boughner & Dean 2004; Boughner 2011). However, because no other juvenile upper jaw specimens are available for *P. boisei*, it remains unclear whether this gap is a derived feature of the species, preventing us from testing this hypothesis.

ONTOGENY OF THE UPPER JAW IN *P. BOISEI*

How morphologically adult is OMO 362-10001?

The derived masticatory system of *Paranthropus* is the most significant argument for its monophyly (Wood 1991; Strait & Grine 2004; Mongle *et al.* 2023). There is strong interest in studying the ontogenetic patterns underlying the development of this morphology, both to challenge phylogenetic relationships and to provide insights into the life history traits of this genus. To date, the study of ontogeny in *Paranthropus* rests only on infants of *P. robustus*, given the scarcity of material from *P. boisei* (Bromage 1989; Braga 1998; McCollum 2008; Cofran 2014; Kuykendall 2019; Braga *et al.* 2023). Here, evidence from OMO 362-10001 shows that this juvenile specimen of *P. boisei* (at the stage of erupted M¹) shows a complex maxillary morphology combining both adult-like and juvenile-like associated traits. Features, such as the thick anterior palate and anteriorly forward placement of the zygomatic root, exhibit a mature condition and are particularly characteristic of the derived robust morphology observed in adults. In *Paranthropus*, palatal thickening and inferior flexion, as seen in OMO 362-10001, have been suggested as consequences of extreme maxillary rotation, acting as a counter process of posterior hyperplasia (McCollum 1999, 2008). Based on this, evidence from OMO 362-10001 suggests that this process is already well advanced in *P. boisei* by the time of M¹ eruption.

Additionally, dental alveolar thickness, sinus morphology, the rostral extension of the palatine groove to M¹, and the relative position of the incisive foramen also align with an adult-like conformation, revealing a particularly mature morphology of this specimen.

Most of the differences observed with the adult condition are tied to size differences – i.e., palate breadth and overall depth, anterior palate depth, and alveolar height – highlighting ongoing ontogenetic change. Regarding those traits, KNM-WT 17400 – a slightly older but still sub-adult individual (which has not yet erupted M³) exhibits an adult-like morphology, suggesting that the transition to the mature condition for these traits occurs rapidly between the emergence of M¹ and M³.

It is, however, necessary to add that comparisons with adult specimens were conducted under the assumption that they represent the potential adult morphology that OMO 362-10001 could likely reach through its growing process. This assumption may bias our interpretations, as the *P. boisei* hypodigm is known to exhibit substantial craniodental morphological variation (Wood 1991; Wood *et al.* 1994; Suwa *et al.* 1997). It will be possible to control such biases with the future discovery of additional juvenile specimens.

Ontogenetic variations within Paranthropus

The sub-nasal morphology of OMO 362-10001 exhibits a strongly orthognathic conformation, with the premaxilla positioned more vertically than in the adult OH 5 (Fig. 6) or OMO 323-1976-896 (Kimbel *et al.* 2004). This difference from the adult condition fits an immature developmental stage, further supported by the presence of an unfused premaxillary suture. Additional features of the anterior jaw, such as alveolar height and anterior palate depth, also differ from the adult condition, indicating ongoing growth in this region.

This observed growth pattern in OMO 362-10001 contrasts with *P. robustus*, where the adult form of the premaxilla is established early in development – before M¹ eruption – due to the fusion of the incisive suture. This early fusion coincides with the cessation of premaxillary growth, preventing further morphological modifications, and it is suggested as a derived pattern shared with *Homo* (Braga 1998; Braga *et al.* 2023). Additionally, the younger *P. robustus* KW 9000 (M¹ not erupted) exhibits more mature alveolar heights and palate depth than OMO 362-10001 (Table 5). The earlier development of the alveolar-zygomatic process configuration (with a high takeoff and steep wall), as seen in KW 9000, more closely resembles the condition observed in *A. africanus* as seen in the juvenile specimen from Taung (Rak 1983; Braga *et al.* 2023). Based on these traits, the ontogenetic pattern of *P. robustus* appears more similar to *A. africanus* than to *P. boisei* as evidenced by OMO 362-10001.

Building on these observations, we suggest that these discrepancies highlight how similar features reach maturity at different times between these two species, potentially reflecting differences in the developmental modularity of the premaxilla. Thus, until further investigation, and without rejecting the monophyly of the clade *Paranthropus*, which is supported by numerous other features (Wood 1991; Strait & Grine 2004; Kimbel *et al.* 2004), this variability in growth trajectories may indicate a degree of developmental variation within the genus.

Supporting this idea, the premaxilla is often described as an independent evolutionary and ontogenetic module, exhibiting significant variation among African hominins (Villmoare *et al.* 2014; Braga *et al.* 2023). Additionally, differences in the timing of premaxilla development have been observed in *Homo*, with *H. neanderthalensis* showing a delayed fusion of the incisive suture relative to *H. sapiens*. This difference in timing allows for subtle modifications in adult morphology between the two closely related species (Maureille & Bar 1999). Thus, a similar variation in *P. boisei* compared to *P. robustus* is not unlikely. However, given the intraspecific variation in

the timing of incisive suture closure (Braga 1998; Maureille & Braga 2002), hypotheses based on a single specimen must be approached with caution.

Functional morphology and life history traits of P. boisei

Both the thickened anterior palate and the anterior projection of the zygomatic process root are functionally significant, enabling high-magnitude loading and providing a greater mechanical advantage in adults (Smith 1978; Grine 1988; Strait *et al.* 2007; Smith *et al.* 2015a; Weber & Krenn 2017). Therefore, we propose that, independently of other facial traits that remain immature (see above), infants of *P. boisei* were rapidly attaining the derived, adult-like masticatory morphology by the time M¹ emerged. Such pattern is also observed in L 427-7, a juvenile mandible specimen of *P. boisei*, which is of a similar age to OMO 362-10001 (M¹ erupted, while P³ and P⁴ complete crown are still in the crypt, with P³ close to erupt). This specimen exhibits a high robusticity index (RI: breadth of the corpus / height of the corpus at M¹ = 0.73) comparable to that of adult *P. boisei* (RI mean = 0.69; Wood 1991), indicating high mechanical loading, despite it not being a fully grown adult. The KNM-ER 1820 mandible is also described as exhibiting a particularly massive corpus for its young age (Wood 1991). The presence of an adult-like, derived masticatory apparatus in OMO 362-10001, along with a tabular and highly worn deciduous dentition – similar to the wear pattern described in adult permanent teeth – suggests early incorporation of an adult-like diet. These findings supports previous hypotheses that *P. boisei* underwent early weaning, before M¹ eruption (Aiello *et al.* 1991; Wood 1991), as suggested for *P. robustus* and *A. africanus* (Tacail *et al.* 2019).

Thus, the ontogeny of derived facial morphology in *P. boisei* appears to be a complex mix of both shared and derived hominin growth patterns, shaped by species-level selection to produce a functional morphology adapted for a tough diet.

CONCLUSION

This study provided the descriptive and comparative analysis of a juvenile maxilla of *Paranthropus boisei* from the Shungura Formation. Our results indicate that this individual, despite its young ontogenetic age (relatively estimated to 3.5–5 years), possessed a fully functional masticatory apparatus likely adapted to an adult-like diet. This opens a new window into the paleobiology of *P. boisei*, suggesting that this species evolved developmental pathways consistent with its highly derived adult dietary regime. Moreover, its ontogenetic trajectory appears to differ from that of the closely-related taxon *P. robustus*, particularly in the anterior portion of the jaw, where premaxilla-related morphology evidences distinct developmental patterns. These findings offer the first direct insights into upper-jaw ontogeny in *P. boisei*, helping to fill a long-standing gap in the fossil record. Overall, this study contributes to a better understanding of the growth, function, and evolutionary distinctiveness of one of the closest relatives of genus *Homo*.

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Author contributions

Fieldwork and authorizations to perform study: OGRE (JRB, BER).

Design of the study: AT, FG, JRB.

Data collection: AT, FG, JS, JRB.

Analyses: AT.

Interpretations: AT, FG, JRB.

Writing, original draft: AT.

Writing, review & editing: all co-authors.

Competing interests

Leslea Hlusko, Franck Guy and Jean-Renaud Boissérie are Recommenders for *PCI Paleontology*.

Data and materials availability

Once published, access to the original material can be obtained by submitting a request to the Ethiopian Heritage Authority, the final repository of the fossil specimens collected by the Omo Group Research Expedition. Access to

the 3D images and associated digital data is likewise available upon request, subject to authorization by the Ethiopian Heritage Authority. The code used for statistical analyses will be uploaded to GitHub.

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APPENDICES

APPENDIX 1. — Comparative specimens used for anatomical comparison of OMO 36210001 permanent dentition.

Methods	Taxon	Tooth	Specimens	References
Anatomical comparison	<i>Paranthropus boisei</i>	C	KNM-WT 17400 ; KNM-WT 37744; KNM-ER 802; KNM-ER 816	Tobias 1967; Leakey & Walker 1988; Tobias 1991; Wood 1991; Prat <i>et al.</i> 2003; CENIEH collections
		P ³	KNM-WT 17400; KNM-ER 6128; OH 5	
		P ⁴	KNM-CH 1-B; KNM-WT 17400; OH 30; OH 5	
		M ¹	KNM-ER 733; KNM-CH 1-B; KNM-WT 17400; KNM-WT 37747; OH 30; OH 5	
	Omo robust	C	L 398-1699	Suwa 1990; Alemseged <i>et al.</i> 2002
		P ³	L 338x-35; OMO 57-148	
		P ⁴	L 338x-34; L 726-11	
		M ¹	OMO 323-76-896; OMO 18-70-1799; L 50-2	
	<i>Paranthropus robustus</i>	C	none	Robinson 1956; Moggi-Cecchi <i>et al.</i> 2010; CENIEH collections
		P ³	DNH 17; DNH 78; SK 823; SK 24; TM 1517; SK 13	
		P ⁴	DNH 22; DNH 59; SK 28; TM 1517; SK 13	
		M ¹	DNH 4; DNH 39; DNH 70; SK 89; SK 13; KB 5063; TM 1601	
	<i>Homo habilis</i>	M ¹	OH 24; OH 13; OH 16; OH 45; OH 21; KNM-ER 1813	Tobias 1991; Wood 1991
		P ⁴	OH 24; OH 13; OH 16; OH 39; KNM-ER 1813; KNM-ER 1590	
		P ³	OH 16; OH 39	
		C	OH 39; OH 16; KNM-ER 1813; KNM-ER 1805; KNM-ER 1590	
	<i>Homo ergaster</i>	C	KNM-WT 15000	Wood 1991; Walker & Leakey 1993
		P ³	KNM-WT 15000	
		P ⁴	KNM-ER 3733; KNM-WT 15000	
		M ¹	KNM-ER 3733	
	Omo gracile	C	L 398-1699	Suwa 1990
		P ³	B 8-23; OMO 33-1971-506; OMO 33-71-740	
		P ⁴	B 7-39B	
		M ¹	OMO Sh 69-17; W8-753; L 51-4; OMO 383-10124a	

APPENDIX 2. — Comparative specimens used for metrical comparison of OMO 362-10001 permanent dentition. Abbreviations: **BL**, bucco lingual; **LL**, labio lingual; **MD**, mesio distal.

Species	ID	Tooth	MD	BL/LL	Data from
New specimen	OMO 362-10001	C	—	8.3	This study
New specimen	OMO362-10001	P ³	10.6	14.4	This study
New specimen	OMO361-10001	P ⁴	12.7	16.9	This study
New specimen	OMO 362-10001	M ¹ original	14.7	15.5	This study
New specimen	OMO 362-10001	M ¹ rebuilt	14.16	14.7	This study
<i>Paranthropus robustus</i>	SK 4	C	8.9	10.3	Robinson 1956
<i>Paranthropus robustus</i>	DNH 53	C	9.9	10.9	Moggi-Cecchi <i>et al.</i> 2010
<i>Paranthropus robustus</i>	DNH 73	C	8.6	9.2	Moggi-Cecchi <i>et al.</i> 2010
<i>Paranthropus robustus</i>	SK 86	C	8.6	8.8	Robinson 1956
<i>Paranthropus robustus</i>	SK 93	C	8.5	9.6	Robinson 1956
<i>Paranthropus robustus</i>	DNH 17	P ³	7.7	13.4	Robinson 1956
<i>Paranthropus robustus</i>	DNH 78	P ³	9.7	12.8	Robinson 1956
<i>Paranthropus robustus</i>	SK 13	P ³	9.8	13.2	Robinson 1956
<i>Paranthropus robustus</i>	SK 24	P ³	9.6	14.1	Robinson 1956
<i>Paranthropus robustus</i>	SK 33	P ³	10.5	15	Robinson 1956
<i>Paranthropus robustus</i>	SK 823	P ³	10.3	14.2	Robinson 1956
<i>Paranthropus robustus</i>	DNH 22	P ⁴	9.5	13.6	Moggi-Cecchi <i>et al.</i> 2010
<i>Paranthropus robustus</i>	DNH 59	P ⁴	10.1	13.9	Moggi-Cecchi <i>et al.</i> 2010
<i>Paranthropus robustus</i>	SK 13	P ⁴	10.5	15.1	Robinson 1956
<i>Paranthropus robustus</i>	SK 28	P ⁴	10.5	15.3	Robinson 1956
<i>Paranthropus robustus</i>	SK 32	P ⁴	11	15.6	Robinson 1956
<i>Paranthropus robustus</i>	DNH 4	M ¹	14.1	15.2	Moggi-Cecchi <i>et al.</i> 2010
<i>Paranthropus robustus</i>	DNH 14	M ¹	11.6	14.4	Moggi-Cecchi <i>et al.</i> 2010
<i>Paranthropus robustus</i>	DNH 57b	M ¹	12.7	13.6	Moggi-Cecchi <i>et al.</i> 2010
<i>Paranthropus robustus</i>	DNH 60	M ¹	12.5	13.6	Moggi-Cecchi <i>et al.</i> 2010
<i>Paranthropus robustus</i>	KW 10840	M ¹	12.9	14	Braga <i>et al.</i> 2023
<i>Paranthropus robustus</i>	KW 9000	M ¹	15.1	14.8	Braga <i>et al.</i> 2023
<i>Paranthropus robustus</i>	SK 13	M ¹	13.4	15	Robinson 1956
<i>Paranthropus robustus</i>	SK 829	M ¹	13.3	14.4	Robinson 1956
<i>Paranthropus robustus</i>	SK 832	M ¹	14	14.8	Robinson 1956
<i>Paranthropus robustus</i>	SK 838	M ¹	14.3	14.9	Robinson 1956
<i>Paranthropus robustus</i>	SK 89	M ¹	14.6	15	Robinson 1956
<i>Paranthropus boisei</i>	KNMT 37744	C	8.7	9.3	Prat <i>et al.</i> 2003
<i>Paranthropus boisei</i>	KNM-WT 17400	C	8.3	8.2	Leakey & Walker 1988
<i>Paranthropus boisei</i>	OH 5	C	8.8	9.9	Tobias 1991
<i>Paranthropus boisei</i>	OH 30	C	8.4	8.4	Tobias 1991
<i>Paranthropus boisei</i>	OMO 323-76-896	C	11	9.6	Alemseged <i>et al.</i> 2002
<i>Paranthropus boisei</i>	KNM-CH 1	P ³	10.2	13.9	Wood 1991
<i>Paranthropus boisei</i>	KNM-ER 1804	P ³	11.3	16.1	Wood 1991
<i>Paranthropus boisei</i>	KNM-ER 802	P ³	12	14.2	Wood 1991
<i>Paranthropus boisei</i>	KNM-ER 6128	P ³	10.6	15.3	Wood 1991
<i>Paranthropus boisei</i>	KNM-WT 17400	P ³	10.6	15.05	Wood 1991
<i>Paranthropus boisei</i>	OH 5	P ³	10.9	17	Tobias 1967
<i>Paranthropus boisei</i>	OH 80-2	P ³	10.4	16.2	Dominguez-Rodrigo <i>et al.</i> 2013
<i>Paranthropus boisei</i>	KNM-CH 1	P ⁴	11.6	15.8	Wood 1991
<i>Paranthropus boisei</i>	KNM-ER 1804	P ⁴	12.1	17.3	Wood 1991
<i>Paranthropus boisei</i>	KNM-ER 6128	P ⁴	10.5	15.2	This Study
<i>Paranthropus boisei</i>	KNM-WT 17400	P ⁴	11.75	15.65	Wood 1991
<i>Paranthropus boisei</i>	OH 5	P ⁴	11.9	17.8	Tobias 1967
<i>Paranthropus boisei</i>	HCRP RC 911	M ¹	14.2	17.5	Kullmer <i>et al.</i> 1999
<i>Paranthropus boisei</i>	KGA10-506	M ¹	14.5	15.9	Suwa <i>et al.</i> 1997
<i>Paranthropus boisei</i>	KNM-CH 1	M ¹	14.2	14.9	Wood 1991
<i>Paranthropus boisei</i>	KNM-ER 1804	M ¹	15.4	16.3	This study
<i>Paranthropus boisei</i>	KNM-ER 733	M ¹	15.6	16.3	This study
<i>Paranthropus boisei</i>	KNM-WT 17400	M ¹	13.65	15.65	Wood 1991
<i>Paranthropus boisei</i>	KNM-WT 37747	M ¹	14.6	15.9	Prat <i>et al.</i> 2003
<i>Paranthropus boisei</i>	OH 5	M ¹	15.2	17.7	Tobias 1967
<i>Homo erectus</i>	KNMWT 15000	C	10.45	11.35	This study
<i>Homo erectus</i>	Bpg 2001.04	P ³	8.1	11.3	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	D 2700	P ³	8.6	11.6	Martín-Torres <i>et al.</i> 2008
<i>Homo erectus</i>	KNM-ER 1808	P ³	8.5	12.8	This study
<i>Homo erectus</i>	KNM-ER 3733	P ³	8.5	12	This study
<i>Homo erectus</i>	KNM-WT 15000	P ³	8.7	11.7	Kimbel <i>et al.</i> 1997
<i>Homo erectus</i>	Pithecanthropus IV	P ³	8.4	12.3	Tobias & von Koenigswald 1964
<i>Homo erectus</i>	S 7-27	P ³	7.8	10.4	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	S 7-31	P ³	7.9	10.6	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	S 7-32	P ³	7.9	10.8	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	S 7-35	P ³	8.5	12.2	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	S 7-58	P ³	9.1	11.5	Zaim <i>et al.</i> 2011

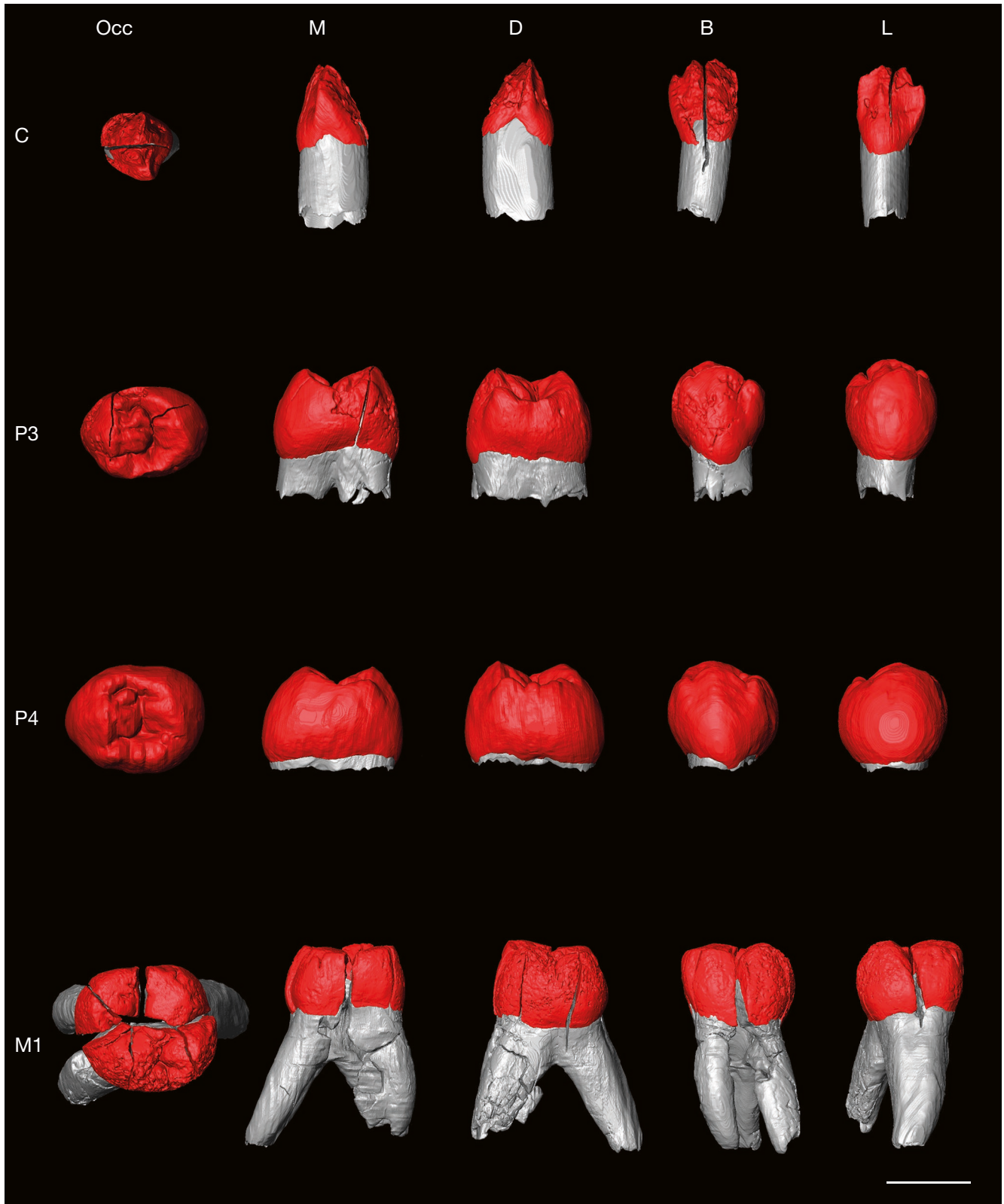
APPENDIX 2. — Continuation.

Species	ID	Tooth	MD	BL/LL	Data from
<i>Homo erectus</i>	Sangiran 15B	P ³	7.5	10.1	Jacob 1973
<i>Homo erectus</i>	Sangiran 16	P ³	7.1	9.9	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	Sangiran 17	P ³	7.2	10.6	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	Sangiran 27	P ³	8.9	12.8	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	Sangiran 4	P ³	8.4	12.4	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	Sh.y. 003	P ³	8.7	12.4	Xing <i>et al.</i> 2016
<i>Homo erectus</i>	Bpg 2001.04	P ⁴	7.6	12.2	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	D 2700	P ⁴	7	11.5	Martinón-Torres <i>et al.</i> 2008
<i>Homo erectus</i>	KNM-ER 3733	P ⁴	8.1	12.1	Kimbel <i>et al.</i> 1997
<i>Homo erectus</i>	KNM-WT 15000	P ⁴	8.3	11.75	Walker & Leakey 1993
<i>Homo erectus</i>	PA 636	P ⁴	9.2	12.7	Xing <i>et al.</i> 2021
<i>Homo erectus</i>	Pithecanthropus IV	P ⁴	8.2	12	Tobias & von Koenigswald 1964
<i>Homo erectus</i>	S 7-29	P ⁴	8.2	10.3	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	S 7-30	P ⁴	7.9	10.2	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	S 7-3a,b,c	P ⁴	7.3	10.2	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	Sangiran 15A	P ⁴	7.8	11	Jacob 1973
<i>Homo erectus</i>	Sangiran 27	P ⁴	7.3	12.4	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	Sangiran 4	P ⁴	8.4	12.2	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	Sh.y. 007	P ⁴	7.9	11.2	Xing <i>et al.</i> 2016
<i>Homo erectus</i>	Sh.y. 0071	P ⁴	8.2	12.3	Xing <i>et al.</i> 2016
<i>Homo erectus</i>	Bpg 2001.04	M ¹	12.5	13.5	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	D 2700	M ¹	12.98	12.2	Martinón-Torres <i>et al.</i> 2008
<i>Homo erectus</i>	D 2710	M ¹	13	12.9	Martinón-Torres <i>et al.</i> 2008
<i>Homo erectus</i>	KGA 11-350	M ¹	12	12.8	Suwa <i>et al.</i> 2007
<i>Homo erectus</i>	KNM-WT 15000	M ¹	12.2	12.2	Kimbel <i>et al.</i> 1997
<i>Homo erectus</i>	PA 637	M ¹	12.9	13.9	Xing <i>et al.</i> 2021
<i>Homo erectus</i>	Pithecanthropus IV	M ¹	12.1	13.6	Tobias & von Koenigswald 1964
<i>Homo erectus</i>	S 7-10	M ¹	11.6	12	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	S 7-37	M ¹	11.4	12.5	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	S 7-38	M ¹	12.8	13.9	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	S 7-3a,b,c	M ¹	11	12.5	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	S 7-40	M ¹	13.6	13.8	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	S 7-8	M ¹	11.5	12.6	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	S 7-9	M ¹	12	13.4	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	Sangiran 17	M ¹	10.8	12.6	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	Sangiran 27	M ¹	11.9	14.5	Zaim <i>et al.</i> 2011
<i>Homo erectus</i>	Sangiran 4	M ¹	12.2	13.6	Zaim <i>et al.</i> 2011
<i>Homo habilis</i>	AL 666-1	C	10.4	10.2	Kimbel <i>et al.</i> 1997
<i>Homo habilis</i>	KMER 803	C	9.3	8.5	Walker & Leakey 1993
<i>Homo habilis</i>	OH 15	C	10.5	11.8	Tobias 1991
<i>Homo habilis</i>	OH 16	C	10	9.8	Tobias 1991
<i>Homo habilis</i>	OH 39	C	9.5	9.1	Tobias 1991
<i>Homo habilis</i>	AL 666-1	P ³	9.2	12.5	Kimbel <i>et al.</i> 1997
<i>Homo habilis</i>	KNM-ER 1506	P ³	8.3	11.9	Wood 1991
<i>Homo habilis</i>	KNM-ER 1590	P ³	10.5	13.55	Wood 1991
<i>Homo habilis</i>	KNM-ER 1805	P ³	8.1	11.75	Wood 1991
<i>Homo habilis</i>	KNM-ER 1813	P ³	8.1	11.3	Wood 1991
<i>Homo habilis</i>	KNM-ER 808	P ³	8.8	12.5	Wood 1991
<i>Homo habilis</i>	OH 13	P ³	9.1	11.25	Tobias 1991
<i>Homo habilis</i>	OH 16	P ³	10	12.25	Tobias 1991
<i>Homo habilis</i>	OH 24	P ³	9.5	12.2	Tobias 1991
<i>Homo habilis</i>	OH 39	P ³	8.85	11.1	Tobias 1991
<i>Homo habilis</i>	OH 65	P ³	9.3	12.7	Blumenschine <i>et al.</i> 2003
<i>Homo habilis</i>	AL 666-1	P ⁴	9	12.6	Kimbel <i>et al.</i> 1997
<i>Homo habilis</i>	KNM-ER 1506	P ⁴	9	12.1	This study
<i>Homo habilis</i>	KNM-ER 1590	P ⁴	10.7	13.7	This study
<i>Homo habilis</i>	KNM-ER 1805	P ⁴	8.6	11	This study
<i>Homo habilis</i>	KNM-ER 1813	P ⁴	8.7	11.4	This study
<i>Homo habilis</i>	OH 13	P ⁴	8.9	11.4	Tobias 1991
<i>Homo habilis</i>	OH 16	P ⁴	9.85	12.05	Tobias 1991
<i>Homo habilis</i>	OH 24	P ⁴	10.2	12.5	Tobias 1991
<i>Homo habilis</i>	OH 39	P ⁴	8.6	10.95	Tobias 1991
<i>Homo habilis</i>	OH 65	P ⁴	9.05	13.05	Blumenschine <i>et al.</i> 2003
<i>Homo habilis</i>	AL 666-1	M ¹	12.9	12.4	Kimbel <i>et al.</i> 1997
<i>Homo habilis</i>	KNM-ER 1590	M ¹	14.1	14.2	This study
<i>Homo habilis</i>	KNM-ER 1805	M ¹	13.2	13.2	This study
<i>Homo habilis</i>	KNM-ER 1813	M ¹	12.1	12.6	This study
<i>Homo habilis</i>	KNM-ER 807	M ¹	12.6	13.8	Kimbel <i>et al.</i> 1997
<i>Homo habilis</i>	OH 13	M ¹	12.8	12.7	Tobias 1991
<i>Homo habilis</i>	OH 16	M ¹	14.7	13.7	Tobias 1991

APPENDIX 2. — Continuation.

Species	ID	Tooth	MD	BL/LL	Data from
<i>Homo habilis</i>	OH 21	M ¹	12.2	11.9	Tobias 1991
<i>Homo habilis</i>	OH 24	M ¹	13.5	13.15	Tobias 1991
<i>Homo habilis</i>	OH 39	M ¹	11.2	12	Tobias 1991
<i>Homo habilis</i>	OH 41	M ¹	13.3	14.1	Tobias 1991
<i>Homo habilis</i>	OH 44	M ¹	12.9	12.6	Tobias 1991
<i>Homo habilis</i>	OH 45	M ¹	13.5	13.1	Tobias 1991
<i>Homo habilis</i>	OH 6	M ¹	13.3	12.4	Tobias 1991
<i>Homo habilis</i>	OH 65	M ¹	12.75	13.55	Blumenschine <i>et al.</i> 2003

APPENDIX 3. — Anatomical plate of OMO 362-10001 permanent dentition. From top to bottom: canine (C), third premolar (P³), fourth premolar (P⁴), first molar (M¹). From left to right: occlusal (Occ), mesial (M), distal (D), buccal (or labial) (B), and lingual (L) views. The first plate shows the crown (red) and roots (grey) of each tooth; the second plate shows dentine and roots. Scale bar: 10 mm.



APPENDIX 4. — Anatomical plate of OMO 362-10001 permanent dentition enamel dentine junction and roots. From top to bottom: canine (**C**), third premolar (**P³**), fourth premolar (**P⁴**), first molar (**M¹**). From left to right: occlusal (**Occ**), mesial (**M**), distal (**D**), buccal (or labial) (**B**), and lingual (**L**) views. Scale bar: 10 mm.

