

Taxonomic assignments for the 3.4 Ma to 1.1 Ma hominin postcanine teeth from the Usno Formation and the Shungura Formation, Lower Omo Valley, Ethiopia

Attributions taxinomiques de la denture jugale des hominines des formations d'Usno et de Shungura (3,4 Ma – 1,1 Ma), basse vallée de l'Omo, Éthiopie

Taxonomic study of the Omo hominin dentition

Leslea J. HLUSKO*

Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Paseo Sierra de Atapuerca 3, 09002 Burgos, Spain

leslea.hlusko@cenieh.es

*corresponding author

Franck GUY

Laboratory Paleontology Evolution Paleoecosystems Paleoprimatology (PALEVOPRIM), CNRS & Université de Poitiers, 86000 Poitiers, France

franck.guy@univ-poitiers.fr

Mario MODESTO-MATA

Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Paseo Sierra de Atapuerca 3, 09002 Burgos, Spain

and

Universidad Internacional de La Rioja (UNIR), Av. de la Paz 137, 26006 Logroño, La Rioja, Spain

mario.modesto@cenieh.es

Marina MARTINEZ DE PINILLOS

Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Paseo Sierra de Atapuerca 3, 09002 Burgos, Spain

and

Laboratorio de Evolución Humana (LEH), Universidad de Burgos, Plaza Misael Bañuelos s/n, 09001 Burgos, Spain

marina.martinez@cenieh.es

Marianne F. BRASIL

Department of Anthropology, Western Washington University, Bellingham, WA 98225

mariannefbrasil@gmail.com

Ian TOWLE

Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Paseo Sierra de Atapuerca 3, 09002 Burgos, Spain

ianetowle@hotmail.co.uk

Arthur THIEBAUT

46 Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Paseo Sierra de Atapuerca 3,
47 09002 Burgos, Spain
48 and
49 Laboratory Paleontology Evolution Paleoecosystems Paleoprimatology (PALEVOPRIM), CNRS & Université
50 de Poitiers, 86000 Poitiers, France
51 arthur.thiebaut@cenieh.es
52
53 **Jean-Renaud BOISSERIE**
54 French Centre for Ethiopian Studies (CFEE), CNRS & Ministry of Europe and Foreign Affairs, PO BOX 5554
55 Addis Ababa, Ethiopia
56 and
57 Laboratory Paleontology Evolution Paleoecosystems Paleoprimatology (PALEVOPRIM), CNRS & Université
58 de Poitiers, 86000 Poitiers, France
59 jean.renaud.boisserie@univ-poitiers.fr

ABSTRACT

Sediments of the Usno Formation and the Shungura Formation date from ca. 3.75 Ma to 1.09 Ma, during which time the genus *Homo* appeared, *Australopithecus* disappeared, and the eastern African robust hominins did both. We performed an in-depth analysis of size, shape, and morphology of 108 Omo permanent postcanine dental specimens. First, we compared linear dimensions against a comparative dataset of 809 teeth from 359 specimens representing 10 hominin taxa. We then developed a linear discriminant function to predict the most-likely taxon for the Omo specimens based on the crown dimensions. We also ran cluster analyses on morphological scores and 2-dimensional cusp areas from the Omo sample to test whether these statistical clusters align with the taxa predicted by the discriminant function analysis. We found that variation in morphological scores does not align well with the taxonomic groups predicted from linear data. Cluster analyses of mandibular molar cusp areas categorize robust and non-robust groups fairly well, but maxillary molar cusp areas do not. We conclude that only *Au. afarensis* is found in the earliest part of the stratigraphy (3.4 Ma). By 2.95 Ma, there are two hominin lineages, *Paranthropus* and a more dentally gracile group in which *Au. afarensis* and *Homo* are not distinguishable until higher in the stratigraphic sequence. *Paranthropus* increased in frequency from 2.27 Ma until 1.9 Ma. After this time, *Homo* is the dominant taxon. The geologically youngest evidence of *Paranthropus* occurs at 1.37 Ma, after which, only teeth attributable to *Homo* are observed.

Keywords: Paleontology, Human evolution, Pliocene, Pleistocene, Africa

RÉSUMÉ

Les sédiments des formations d'Usno et de Shungura sont datées d'environ 3,75 à 1,09 Ma, période pendant laquelle le genre *Homo* apparaît, *Australopithecus* disparaît et les hominines robustes d'Afrique orientale font les deux. Nous avons effectué une analyse approfondie de la taille et de la forme de 108 spécimens dentaires de l'Omo. Tout d'abord, nous avons comparé les dimensions linéaires et la morphologie à un ensemble de données comparatives de 809 dents provenant de 359 spécimens représentant 10 taxa d'hominines. Nous avons ensuite développé une fonction discriminante linéaire pour prédire l'attribution taxinomique la plus probable pour les spécimens de l'Omo en fonction des dimensions de la couronne. Nous avons également effectué des analyses de groupe [analyse en grappes] sur les scores morphologiques et les aires cuspaes 2D de l'échantillon afin de vérifier si les agrégats correspondaient aux taxons prédits par l'analyse discriminante. Nous constatons que la variation sur la base des scores morphologiques correspond peu aux groupes taxinomiques prédits à partir des données linéaires. Les analyses en grappes des aires cuspaes des molaires inférieures catégorisent correctement les groupes robustes et non robustes, contrairement aux molaires supérieures. Nous concluons que seul *Au. afarensis* montre une occurrence dans la partie la plus ancienne de la stratigraphie (3,4 Ma). Vers 2,95 Ma, il existe deux clades d'hominines, *Paranthropus* et un groupe plus gracile sur le plan dentaire au sein duquel *Au. afarensis* et *Homo* ne sont distinguables qu'à des niveaux plus élevés de la séquence stratigraphique. La fréquence des spécimens *Paranthropus* s'accroît de 2,27 à 1,9 Ma. Après cette période, *Homo* est le taxon dominant. Les témoignages les plus récents pour *Paranthropus* sont datés entre 1,5-1,37 Ma. Après cette période, seules des dents attribuables à *Homo* et *H. erectus* sont observées.

Mots clefs : Paléontologie, Évolution humaine, Pliocène, Pléistocène, Afrique

105 INTRODUCTION

107 BACKGROUND

108 The geology of eastern Africa is extraordinary for being tectonically and volcanically active due to its
109 location at the divergence of three continental plates (Schlüter 1997). Over the last few million years, this
110 region experienced a remarkable amount of tectonic movement that exposed the sediments formed by
111 the ever-shifting river and lake systems (WoldeGabriel *et al.* 2000; Brown & McDougall, 2011). Thanks to
112 the frequency of volcanic eruptions, geochronology provides remarkably accurate age estimates of the
113 volcanic ashes and inter-bedded sediments, and consequently, geological ages for the fossils found within
114 them (WoldeGabriel *et al.* 2013; Niespolo *et al.* 2021; Vidal *et al.* 2022).

115 Fortuitously for the study of human evolution, our ancestors lived in this region almost continuously
116 for the last 6 million years (e.g., Haile-Selassie 2001; Senut *et al.* 2001; White *et al.* 2009; Wood and Leakey
117 2011). Three million years ago, the genus *Australopithecus* was firmly established in eastern Africa
118 (Johanson *et al.* 1982; White *et al.* 1993; Kimbel & Delezenne 2009; Ward *et al.* 2012), and likely extended
119 much farther to the west (Brunet *et al.* 1995; Brunet *et al.* 1996; Guy *et al.* 2008) and into southern Africa
120 (Moggi-Cecchi *et al.* 2006; Clark & Kuman 2019; Beaudet 2023). At some point over the next million years,
121 the genus *Homo* evolved, but from what type of earlier hominin species is still debated (e.g., McHenry &
122 Coffing 2000; Kimbel 2009; Antón & Snodgrass 2012; Kimbel & Villmoare 2016; Du & Alemseged 2019;
123 Davies *et al.* 2020). By 1 Ma, the genus *Homo* appears to be the sole remaining member of the Hominini.
124 The intervening two-million-years saw the rise and fall of a dentognathically robust hominins in eastern
125 Africa that are referred to as chronospecies either within the genus *Australopithecus* or within the genus
126 *Paranthropus*, depending on the evolutionary scenario interpreted (Grine 1988; Strait *et al.* 1997; Wood
127 & Constantino 2007; Strait 2013; Lacruz *et al.* 2019).

128 Although hominins appear to have been rare and generally scarce compared to other terrestrial
129 vertebrates (Leakey & Werdelin 2010; Maclatchy 2010), some terrestrial fossil sites in eastern Africa have
130 yielded evidence of sympatric penecontemporaneous hominin species (e.g., Leakey & Walker 1976; Suwa
131 *et al.* 1996; Haile-Selassie *et al.* 2016b). These examples demonstrate that hominin evolution was not
132 linear. Some researchers now interpret a great degree of taxonomic diversity, although there is significant
133 debate on this point (Foley 2005; White 2009; Spoor *et al.* 2016; Wood & Boyle 2016; Brasil *et al.* 2020;
134 Harvati & Reyes-Centeno 2022). In light of this context, sedimentary sequences that preserve fairly
135 continuous records of continental vertebrate evolution are essential for testing hypotheses about the

amount of diversity within human evolution at various points in geological time and in geographic space, and the biotic and abiotic contexts around that diversity.

OMO

One of the most impressive of these sequential hominin-bearing fossil sites is the Shungura Formation in the southern part of Ethiopia, and the correlated Usno Formation nearby (Fig. 1). The Omo River Basin has long been home to a wide diversity of terrestrial vertebrates. From approximately 3.75 Ma to 1.1 Ma, sediments formed along the paleo Omo River, capturing and fossilizing the remains of animals that died along the river banks and environs. Today, the sediments of the Shungura and Usno Formations are exposed by the Omo River, and the abundant fossils eroding out represent one of the richest records of terrestrial vertebrates from this time period, including a rather intriguing episode of human evolution that marks the beginning of the genus *Homo* and the appearance of hominins with incredibly robust masticatory anatomy (Howell *et al.* 1976; Boissarie *et al.* 2008; Wood & Leakey 2011).

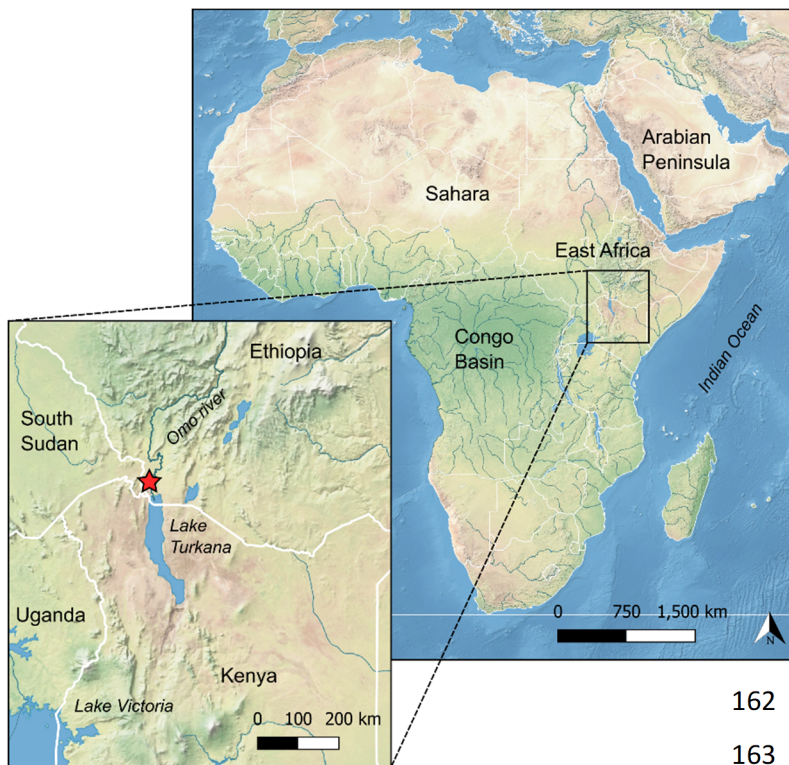


FIG. 1. – Map showing geographic location of the Shungura Formation, Lower Omo Valley, Ethiopia.

Given the geological age-range of the Shungura Formation and how fossiliferous these sediments are, paleoanthropologists have long been interested in its exposures. In 1933, C. Arambourg was the first to conduct fieldwork there. Based on those early discoveries, he and colleagues Y. Coppens, F. C. Howell and L. S. B. Leakey directed the International Omo Research Expedition (IORE) in the Omo from 1967 to 1976

(Coppens *et al.* 1976). In 1967, evidence of a previously unknown robust hominin species, '*Paraustralopithecus*' *aethiopicus* (now typically referred to as *Paranthropus aethiopicus*), was discovered in Omo sediments dating ca. 2.6 Ma (Arambourg & Coppens 1968). At the time, its relationship to the other hominins recovered from eastern African sites, or even with the other hominins from the Omo, was difficult to interpret.

The hominin fossils from the Omo tend to be highly fragmentary, with isolated teeth being the most common elements recovered. Consequently, most publications that describe or refer to hominin remains from the Omo tend to focus on the rarer, more complete specimens, largely ignoring the isolated dental remains that compose the majority of the Omo hominin fossil record. Even comprehensive studies of the hominin dentition shied away (e.g., Wood & Uytterschaut 1987). Consequently, a time-sequence analysis of hominin evolution through the ca. 2.2 million years of evolution recorded within the Usno Formation and Shungura Formation is challenging, as it requires an analysis of isolated teeth, a notoriously difficult task.

In the 1990s, Suwa (1990) and colleagues (Suwa *et al.* 1996) took on the challenge. They focused their taxonomic analysis on 48 isolated mandibular postcanine teeth recovered from the Shungura Formation between 1967 and 1976. By studying linear metrics, 2-dimensional cusp areas, and morphological observations, they differentiated between robust and non-robust categories, finding that the two lineages appear to coexist in the Omo by 2.7 Ma. They concluded that *Paranthropus boisei* is clearly identifiable by 2.3 Ma (referred to as *Australopithecus boisei* in Suwa *et al.* 1996). They find no evidence of multiple species at any one time horizon within the non-robust specimens (Suwa *et al.* 1996). These interpretations have held as the general consensus of numerous subsequent studies (e.g., Bobe & Leakey 2009; Wood and Leakey 2011).

In 2006, Boissarie and colleagues initiated the Omo Group Research Expedition (OGRE; Boissarie *et al.* 2008) and discovered 52 new hominin specimens (2006-2019). Similar to the hominin discoveries of the IORE, the OGRE has recovered further evidence of hominins primarily through isolated dental and partial dentognathic remains. These new fossil assemblages demonstrate that the Omo localities (and their proclivity to yield isolated teeth) will continue to contribute evidence of human evolution across a particularly intriguing time interval. Consequently, our aim in this study is to improve our ability to infer taxonomy from isolated teeth.

BIODIVERSITY, PHYLETIC EVOLUTION, AND TAXONOMY

Since the last (and only) in-depth studies of the isolated hominin teeth from the Shungura Formation (Suwa 1990; Suwa *et al.* 1996), there have been numerous fossil discoveries that dramatically improve and influence our understanding of hominin evolution. For example, we now have fossils that anchor the dental variation of the Late Miocene hominins (Senut *et al.* 2001; Haile-Selassie 2001; Brunet *et al.* 2002; Haile-Selassie *et al.* 2004), provide knowledge of the Pliocene hominin dentitions prior to *Australopithecus afarensis* (White *et al.* 1994; Leakey *et al.* 1995; Kimbel & Lockwood 2006; White *et al.* 2006; Suwa *et al.* 2009; Haile-Selassie *et al.* 2019), permit a deeper understanding of the range of variation penecontemporaneous to *Au. afarensis* (Brunet *et al.* 1995; Asfaw *et al.* 1999; Haile-Selassie *et al.* 2015; Leakey *et al.* 2001), and broaden the geographical context for early *Homo* (e.g., Martín-Torres *et al.* 2007a,b; Martín-Torres *et al.* 2008; Macaluso 2010; Martín-Torres *et al.* 2012; Bermúdez de Castro *et al.* 2011, 2019, 2021, 2024). An overview of these discoveries is summarized in Fig. 2 alongside the Shungura Formation sequence.

This increased biodiversity of hominin taxa provides an expanded list of possible genera and species that represent testable taxonomic hypotheses for the isolated teeth from the Omo. Table 1 presents the hominin taxa known from other penecontemporaneous eastern African fossil sites divided into half-million-year increments.

This taxonomic diversity also poses a significant challenge of semantics. Linnean names are static and cannot embrace the dynamic nature of evolution. We know that evolution is, by definition, change over time, and that this change occurs at different rates at different times. And yet, because of the nature of language, we have to designate taxonomic names to discrete sections of dynamically evolving lineages. Even the use of chronospecies and chronosubspecies force subjective delimitation. This is especially problematic when we have a fairly continuous record of evolution, such as what the sedimentary sequences exposed in the Omo River Valley offer.

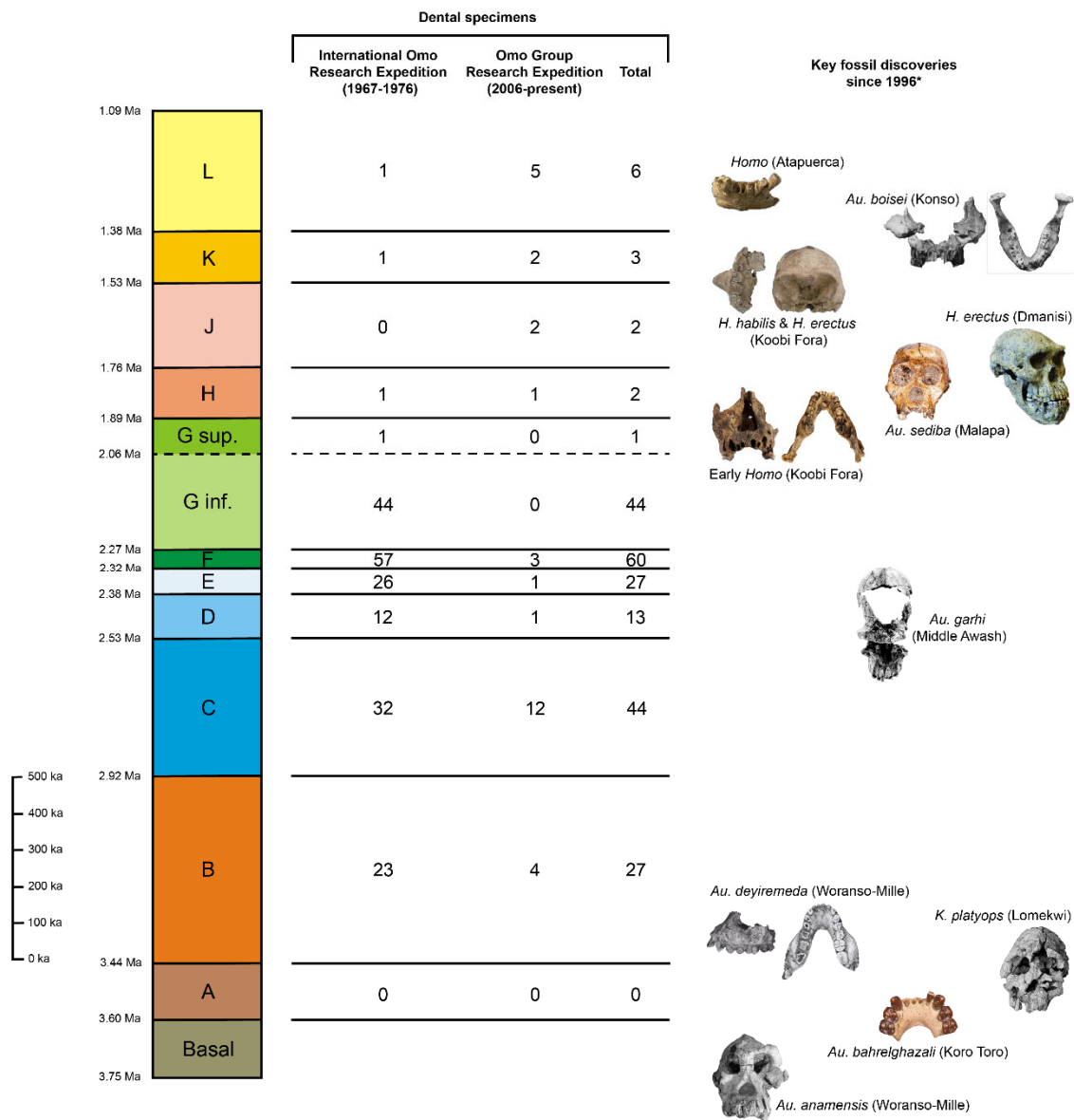
While there is a rich literature on the biological meaning of taxonomic classification (e.g., De Queiroz 2005, 2007; Kuntner & Agnarsson 2006), here, we focus on the role that taxonomic labels play in categorizing morphology. This categorization is essential to our ability to investigate anatomical evolution as it allows the scientific community to communicate with each other efficiently. In this study, we use taxonomy in this manner, for purposes of communication. We follow the phylogenetic systematic practice of including *Pan*, *Gorilla*, *Homo*, and their ancestors in the Linnean Subfamily Homininae, and classifying all genera along the human clade since its split with chimpanzees within the Tribe Hominini. We do this

to make it easier for readers to align our taxonomy with the current predominant taxonomic practice in the scientific literature. However, while doing this, we note that the biological implications of this taxonomy are a significant topic of debate. The authors do not have agreement on the biological relevance of these Linnean categorical distinctions. Additionally, we use genus and species names that are widely employed in the paleoanthropological community. Our use of these terms is not indicative of our conclusion that the distinctions are biologically valid nor that other taxonomic practices are invalid. The specific details are described in the Materials section, but we raise this issue here to remind the reader of the multipurpose use of taxonomic names in order to avoid misinterpreting the current taxonomic discussion with one about hominid and hominin paleobiology.

TABLE 1. – Known hominin taxa from eastern Africa between 4.0 Ma and 0.5 Ma.

Geological Age (Ma)	Genus and species
0.5 to 1.0 Ma	<i>Homo erectus</i>
1.0 to 1.5 Ma	<i>Paranthropus boisei</i> <i>Homo habilis</i> <i>Homo ergaster</i>
1.5 to 2.0 Ma	<i>Paranthropus boisei</i> <i>Homo habilis</i> <i>Homo ergaster</i>
2.0 to 2.5 Ma	<i>Paranthropus boisei</i> <i>Paranthropus aethiopicus</i> <i>Homo habilis</i>
2.5 to 3.0 Ma	<i>Paranthropus aethiopicus</i> <i>Homo habilis</i> <i>Australopithecus garhi</i>
3.0 to 3.5 Ma	<i>Australopithecus afarensis</i> <i>Australopithecus deyiremeda</i> <i>Kenyanthropus platyops</i>
3.5 to 4.0 Ma	<i>Australopithecus afarensis</i> <i>Australopithecus anamensis</i>

FIG. 2. – Omo stratigraphy and key non-Omo fossil discoveries (since 1996) from between ca. 3.8 Ma and 1.2 Ma that have been published since the most recent description of dental remains from the Omo (Suwa *et al.* 1996). Fossil images are adapted from published sources, as follows, listed from geologically youngest to oldest: mandible of *Homo* from Atapuerca, Spain (Bermúdez de Castro *et al.* 2011); first skull of *Au. boisei*, from Konso, Ethiopia (Suwa *et al.* 1997); new fossils published as *H. habilis* and *H. erectus* from Koobi Fora, Kenya (Spoor *et al.* 2007); complete skull of *H. erectus* from Dmanisi, Georgia (Lordkipanidze *et al.* 2013); *Au. sediba* described as a new species from Malapa, South Africa (Berger *et al.* 2010); new fossils of early *Homo* from Koobi Fora, Kenya (Leakey *et al.* 2012); *Au. garhi* described as a new species from Middle Awash, Ethiopia (Asfaw *et al.* 1999); *Au. deyiremeda* described as a new species from Woranso-Mille, Ethiopia (Haile-Selassie *et al.* 2015); *K. platyops* described as a new genus and species from Lomekwi, Kenya (Leakey *et al.* 2001); *Au. bahrelghazali* described as a new species from Koro Toro, Chad (Gibbons 2012; and see Brunet *et al.*, 1995); new cranium of *Au. anamensis* from Woranso-Mille, Ethiopia (Haile-Selassie *et al.* 2019).



MATERIALS

THE OMO FOSSILS

The hominin dental assemblage from the Shungura Formation and Usno Formation used in this study derives from two field expeditions. The IORE took place between 1967 and 1976 (Howell *et al.* 1976) and yielded 197 isolated teeth, 48 of which were included in Suwa *et al.* (1996)'s previous study of the mandibular postcanine dentition. Between 2006 and 2018, fieldwork conducted by OGRE (Boisserie *et al.* 2008) recovered 45 of the hominin dental remains studied herein. We included in our analyses specimens that are complete enough to measure both crown mesiodistal and buccolingual width and/or to permit full morphological scoring, with a few exceptions. We focus only on the postcanine dentitions of the maxilla and mandible. Incisors and canines are not included in this analysis but instead will be described elsewhere. In total, 132 hominin teeth representing 108 specimens from the Omo Shungura Formation are the subject of this study (Table 2). Of these specimens, 84 were recovered by IORE and 24 by OGRE. We do not include the OGRE 2019 and later discoveries because we have not had the opportunity to study them fully in person due to the timing of the COVID-19 pandemic. More complete dentognathic specimens will be published separately.

Most of these 108 specimens are from the Shungura Formation. However, 10 specimens were recovered from Unit U-12 of the Usno Formation, four from the Brown Sands (B numbers) and six from the White Sands (W numbers). This level of the Usno Formation is correlated to Unit B-2 of the Shungura Formation, and therefore these specimens are presented alongside those from the B-2 Shungura unit.

These 108 fossil specimens were studied in-person at the Ethiopian Heritage Authority/National Museum of Ethiopia in Addis Ababa in 2019 by two of the authors (L.J.H., F.G.). Linear measurements and initial descriptions were collected from the fossils by L.J.H. Photographs were taken by F.G. using a Nikon camera. Each specimen was mounted on a rotating plane (turn-table) and photographed in numerous orientations relative to the light source so that structures were variously highlighted. Subsequent analysis was conducted using the photographs of the original fossils and high-resolution plaster replicas of the IORE and OGRE tooth crowns that are available at both the CENIEH and at the University of Poitiers. Some specimens were photographed again in May 2024 for Supplemental Figure S1, a presentation of the occlusal view of all 108 Omo specimens.

Thirteen of the Omo specimens were included in the comparative dataset based on their previous taxonomic identifications. These 13 specimens (with a total of 16 teeth) have repeatedly been referred to

as *P. aethiopicus*. Therefore, we included these specimens in our comparative dataset to represent *P. aethiopicus* (Table 3).

TABLE 2. – List of Omo specimens included in this study.*

Specimen inventory	Dental element	Metric LDA	Morph Scores	Cusp Area	Strat Level	Final taxonomic assignment
B 7-39	lt P ³ , lt P ⁴	X	X		correlated to B-2	<i>Australopithecus</i> LP
B 8-4Q	lt P ⁴ (germ)	X	X		correlated to B-2	<i>Australopithecus</i> LP
B 8-14B	lt P ⁴	X			correlated to B-2	<i>Australopithecus</i> LP
B 8-23	lt P ⁴ , lt M ³	X	X	X	correlated to B-2	<i>Australopithecus</i> LP
W 7-23	lt P ₄	X	X		correlated to B-2	<i>Australopithecus</i> LP
W 7-508	rt M ₁	X	X	X	correlated to B-2	<i>Au. LP/Homo</i> EEA
W 8-749	rt M ¹	X	X	X	correlated to B-2	<i>Australopithecus</i> LP
W 8-752	rt M ₁	X			correlated to B-2	<i>Au. LP/Homo</i> EEA
W 8-988	lt P ⁴	X	X		correlated to B-2	<i>Australopithecus</i> LP
W-978	rt P ₃	X	X		correlated to B-2	<i>Australopithecus</i> LP
L 1/nn-10010	rt and lt M ₂	X	X	X	B-9	<i>Au. LP/Homo</i> EEA
L 1-294	rt M ₃	X	X	X	B-9 - C	<i>cf. Paranthropus</i>
L 1-398	rt M ₂	X	X	X	B-9 - C	<i>Au. LP/Homo</i> EEA
L 2-89	lt M ₃	X		X	B-10	<i>Au. LP/Homo</i> EEA
L 795-1	rt M ₃	X	X	X	B-12 - C-1	<i>Paranthropus</i>
OMO 28/S-1968-30	rt M ₃	X	X	X	B-9 - B-10	<i>Paranthropus</i>
OMO 112/2-10029	rt M ₂ and M ³	X	X	X	B-9	<i>Au. LP/Homo</i> EEA
OMO 112/4-10009	lt P ³	X	X		B-10	<i>Australopithecus</i> LP
OMO 212-1973-1950	lt M ₁ germ	X	X		B-10	<i>Au. LP/Homo</i> EEA
OMO 212-10012	rt P ⁴	X	X		B-10	<i>Australopithecus</i> LP
L 45-2	rt M ₁	X	X	X	C-5	<i>Au. LP/Homo</i> EEA
L 51-1	lt M ₁	X	X	X	C-9	<i>Au. LP/Homo</i> EEA
L 51-2	lt M ¹	X	X	X	C-9	<i>Au. LP/Homo</i> EEA
L 51-3	lt M ²	X	X		C-9	<i>Au. LP/Homo</i> EEA
L 51-4	lt M ¹	X	X	X	C-9	<i>Au. LP/Homo</i> EEA
L 51-79	rt P ₄	comparative specimen			C-9	<i>P. aethiopicus</i>
L 51-80	rt P ₄	X	X		C-9	<i>Au. LP/Homo</i> EEA
L 51-10002	rt M ₃	X	X	X	C-9	<i>Au. LP/Homo</i> EEA
L 55-33	lt P ₄ (in mand frag)	comparative specimen			C-6	<i>P. aethiopicus</i>
L 62-17	rt M ₂	comparative specimen			C 4 - C 6	<i>P. aethiopicus</i>
L 220-10001	rt M ³	X	X		C-6	<i>Au. LP/Homo</i> EEA
OMO 18-1968-31	lt P ₃	comparative specimen			C-8	<i>P. aethiopicus</i>
OMO 18-1968-33	lt P ₃	X	X		C-8	<i>Au. LP/Homo</i> EEA
OMO 18-1968-34	lt M ₁	comparative specimen			C-8	<i>P. aethiopicus</i>
OMO 18-1970-1799	lt M ²	X	X	X	C-8	<i>Paranthropus</i>
OMO 69-1974-900	lt P ⁴	X	X		C-8	<i>Au. LP/Homo</i> EEA
OMO 84-10001	lt M ¹	X	X	X	C or F (uncertain)	<i>cf. Homo</i>
OMO 157-10009	lt M ₃	X	X	X	C-5	<i>Au. LP/Homo</i> EEA
OMO 163-10001	rt M ³ germ	X	X	X	C-6	<i>Au. LP/Homo</i> EEA
OMO 224-10005	rt M ₂	X	X	X	C-7	<i>Au. LP/Homo</i> EEA
OMO 329-10015	rt M ₃ germ	X	X	X	C-8	<i>Au. LP/Homo</i> EEA
OMO 349-10003	lt M ₂	X	X		C-4	<i>Au. LP/Homo</i> EEA

TABLE 2 (following). – List of Omo specimens included in this study.*

Specimen inventory	Dental element	Metric LDA	Morph Scores	Cusp Area	Strat Level	Final taxonomic assignment
L 9-12	lt M ³	X	X	X	D-upper	<i>Paranthropus</i>
L 50-2	lt M ²	X	X	X	D	<i>Paranthropus</i>
L 441-10001	lt P ³	X	X		D-1	<i>Au. LP/Homo</i> EEA
L 824-5	lt M ₁	X			D-1	<i>Au. LP/Homo</i> EEA
L 26-1G	rt M ₁	X	X	X	E-2	<i>Au. LP/Homo</i> EEA *
L 338/X-34	lt M ²	X	X	X	E-3	<i>Paranthropus</i>
L 338/X-35	rt P ³	X	X		E-3	<i>P. boisei</i>
L 338/X-39	lt M ₃	comparative specimen			E-3	<i>P. aethiopicus</i>
L 338/X-40	lt P ₄	comparative specimen			E-3	<i>P. aethiopicus</i>
OMO 57/3-10010	rt M ₂	X	X	X	E-3	<i>Au. LP/Homo</i> EEA
OMO 166-1973-781	lt M ³	X	X	X	E-1	<i>Au. LP/Homo</i> EEA *
OMO 177-1973-4525	rt P ₃	X	X		E-3 - E-5	<i>Australopithecus</i> LP
F 22-1	rt M ₂ and rt M ₃	comparative specimen			F-1	<i>P. aethiopicus</i>
L 28-30	rt M ₃	X	X	X	F-1	cf. <i>Homo</i>
L 28-58	rt M ¹	X	X		F-1	<i>Homo</i>
L 157-35	lt M ₂	comparative specimen			F-0 or F-1	<i>P. aethiopicus</i>
L 238-35	rt M ²	X	X	X	F-2	cf. <i>Au. garhi</i>
L 398-120	rt P ₃	comparative specimen			F-0	<i>P. aethiopicus</i>
L 398-573	lt M ³	X	X		F-0	<i>Au. LP/Homo</i> EEA
L 398-630	rt M ₃				F-0	<i>Paranthropus</i>
L 398-2608	rt M ³	X	X	X	F-0	<i>Au. LP/Homo</i> EEA
L 860-2	mand with lt P ₃ , lt P ₄ , rt P ₃ , rt M ₂	comparative specimen			F-1	<i>P. aethiopicus</i>
OMO 33-1969-9	rt M ₃	comparative specimen			F-0	<i>P. aethiopicus</i>
OMO 33-1970-63	rt M ³	X	X		F-0	<i>Au. LP/Homo</i> EEA
OMO 33-1971-506	rt P ³	X			F-0	<i>Au. LP/Homo</i> EEA
OMO 33-1971-508	rt P ₄	comparative specimen			F-0	<i>P. aethiopicus</i>
OMO 33-1973-3282	lt P ⁴	X	X		F-0	<i>Au. LP/Homo</i> EEA
OMO 33-1973-5496	lt P ₃	X			F-0	<i>Au. LP/Homo</i> EEA
OMO 123/N-1973-5495	rt P ₃	X	X		F-3	cf. <i>Homo</i>
OMO 174-10002	lt M ₃	X	X	X	F-2 - F-3	<i>Homo</i>
OMO 371-10035	lt M ₃	X	X	X	F	<i>Homo</i>
P 933-1	lt M ¹	X	X		F-3	<i>Homo</i>
L 7-279	lt M ₂	X			G-4 - G-8	<i>Homo</i>
L 7/A-125	mand with lt P ₄ , and lt & rt M ₃	X			G-4 - G-8	<i>P. boisei</i>
L 74/A-21	mand with rt P ₄	X	X		G-3 - G-5	<i>Paranthropus</i>
L 427-7	mand with rt P ₃ & M ₂	X	X		G-4	<i>Paranthropus</i>
L 628-1	lt P ₄	X	X		G-3	<i>Paranthropus</i>
L 628-2	rt M ₃ frag				G-3	<i>Paranthropus</i>
L 628-3	lt M ₃	X	X	X	G-3	<i>Paranthropus</i>

TABLE 2 (following). – List of Omo specimens included in this study.*

Specimen inventory	Dental element	Metric LDA	Morph Scores	Cusp Area	Strat Level	Final taxonomic assignment
L 628-4	lt P ₄	X	X		G-3	<i>cf. Paranthropus</i>
L 628-9	lt M ₁	X	X	X	G-3	<i>Paranthropus</i>
L 628-10	lt M ₂				G-3	<i>cf. Paranthropus</i>
L 726-11	rt P ⁴ frag				G-5	hominin
L 894-1	rt P ³ , rt P ⁴ , rt M ¹ , rt and lt M ³	X	X		G-27 - G28	<i>Au. LP/Homo</i> EEA
OMO Sh 1/1-1969-17	lt M ¹	X		X	G-8 - G-9	<i>Homo</i>
OMO 29/1-1968-43	rt P ₃	X	X		G-6 - G-13	<i>cf. Homo</i>
OMO 47-1968-46	rt M ₂ frag				G-8	<i>P. boisei</i>
OMO 47-1973-1500	rt M ₂	X	X	X	G-8	<i>P. boisei</i>
OMO 75-1969-14	lt and rt P ₃ , rt P ₄ , rt M ₁ , lt and rt M ₂ , lt M ₃ , lt P ⁴ , rt M ³	X	X		G-4 - G-13	<i>Homo</i>
OMO 75/i-1970-1255	rt P ₃		X		G-3 - G-8	<i>Homo</i>
OMO 75/S-1969-15	lt M ₁	X	X		G-1 - G-13	<i>cf. Homo</i>
OMO 75/S-1969-16	rt M ₃	X	X	X	G-1 - G-13	<i>Homo</i>
OMO 136-1972-1	lt M ₃	X	X		G-1	<i>Paranthropus</i>
OMO 136-1972-2	lt M ₂	X			G-1	<i>cf. Paranthropus</i>
OMO 195-1973-1630	rt M ₁	X			G-7	<i>Homo</i>
OMO 74-1969-18	rt P ₄ germ		X		H-4 - H-6	<i>cf. Homo</i>
OMO VE 3-10011	lt M ₃		X	X	H-5	<i>Homo</i>
OMO 352-10086	lt M ₁	X	X	X	J-4	<i>P. boisei</i>
F 203-1	rt M ₂	X	X	X	K-4	<i>Paranthropus</i>
OMO 343-10001	M ³ distal frag				K-3	<i>Au. LP/Homo</i> EEA
OMO 362-10039	rt P ⁴	X	X		K-2	<i>Au. LP/Homo</i> EEA
OMO 342-10126b	rt M ₁ germ	X	X	X	L-9	<i>Homo</i>
OMO 382-10008	frag lt M ₃				L	<i>Paranthropus</i>
OMO 383-10124	lt M ¹ and M ²	X	X	X	L	<i>H. erectus</i>
OMO 389-10085	rt M ₃	X			L	<i>H. erectus</i>
OMO K 7-1969-19	lt M ₂	X	X	X	L-9	<i>cf. Homo</i>

*For specific details on individual teeth from the same specimen see Supplemental Table S1.

COMPARATIVE DATASET

The comparative dataset for our metric analysis was culled from the published literature by L.J.H. with assistance from M.M.M, I.T., M.M.P., and A.T. In total, 359 specimens are included, representing 809 teeth. Specimens are listed by taxonomic category in Table 3 and by tooth count and position in Table 4. We keep *Au. deyiremeda* separate in the species-level analyses. However, given the high degree of overlap in size and shape with *Au. afarensis* and the small number of individuals attributed to other Late Pliocene species, we use a taxonomic category that we call “*Australopithecus* Late Pliocene” (*Australopithecus* LP, or *Au. LP*) that includes *Australopithecus afarensis*, *Au. bahrelghazali*, and *Kenyanthropus platyops*. We also combine all of the fossils from eastern Africa that have been identified to early *Homo*, such as *H.*

habilis and *H. rudolfensis*, into one category called “*Homo* early eastern Africa” (*Homo* EEA). While this grouping of different taxa may seem to potentially obscure taxonomic distinctions, we found that the taxa within each of these categories have a significant degree of morphological overlap in their dental variation. Therefore, these larger taxonomic categories are more useful than species-level divisions.

For our comparative sample, when the source from which we culled the measurements included an estimation of the mesiodistal length that corrected for interproximal wear, we used this reconstructed length estimate. Our aim is to capture the biological potential and variation observed within each taxon. In contrast, our measurements of the Omo fossils record the actual mesiodistal length as we did not attempt to correct for interstitial wear. We excluded measurements from overly-worn (>1mm) Omo teeth. Consequently, our mesiodistal dimensions are, by and large, within a millimeter of the actual crown mesiodistal length. The reader is cautioned to place a buffer around the edges of the observed variation for both the comparative and our Omo mesiodistal measurements.

We did not include P_3 mesiodistal or buccolingual dimensions for the two species of *Ardipithecus* nor for *Au. anamensis* in our comparative analyses. The morphology of these early hominin P_3 s is distinct from the later, more derived hominins (Suwa *et al.* 2009 SOM). Consequently, the mesiodistal and buccolingual dimensions are not directly comparable. Therefore, *Ardipithecus* is not included in analyses of P_3 linear metrics. Additionally, the genus-level analyses of P_3 metrics for *Australopithecus* do not include *Au. anamensis*. The exclusion of the linear measurements that capture this ancestral morphology is further justified in that none of the Omo specimens demonstrate this geologically older morphology.

All of our comparative data are published and freely available (**reference Data Dryad DOI once uploaded**). These data consist of measurements taken by T.D. White, L.J. Hlusko, and culled from the following citations (Tobias & Koenigswald 1964; Tobias 1967; Jacob 1973; White 1977, 1980; Johanson *et al.* 1982; Wood & Van Noten 1986; Leakey & Walker 1988; Kyauka & Ndessokia 1990; Tobias 1991; Wood 1991; Schrenk *et al.* 1993; Walker & Leakey 1993; Brunet *et al.* 1995; Gabunia & Vekua 1995; Kimbel *et al.* 1997; Suwa *et al.* 1997; Asfaw *et al.* 1999; Kullmer 1999; White *et al.* 2000; Brown *et al.* 2001; Ward *et al.* 2001; Blumenschine *et al.*, 2003; Prat *et al.* 2003; Kimbel *et al.* 2004; Kaifu *et al.* 2005; Semaw *et al.* 2005; Martín-Torres *et al.* 2008; Haile-Selassie & WoldeGabriel 2009; Haile-Selassie *et al.* 2010; Harrison 2011; Zaim *et al.* 2011; Clarke 2012; Leakey *et al.* 2012; Domínguez-Rodrigo *et al.* 2013; Ward *et al.* 2013; Zaolli *et al.* 2014; Haile-Selassie & Melillo 2015; Haile-Selassie *et al.* 2015; Simpson *et al.* 2015; White *et al.* 2015; Haile-Selassie *et al.* 2016; Xing *et al.* 2016; Grine *et al.* 2019; Noerwidi 2020; Skinner *et al.* 2020; Melillo *et al.* 2021; Xing *et al.* 2021).

TABLE 3. – List of the 359 comparative specimens by taxonomic category.

Taxa	N	Specimen inventory numbers				
<i>Ardipithecus kadabba</i>	9	ABD1/P1	ASK-VP-3/160	ASK-VP-3/402	ESC8/P1	STD-VP-2/63
		ALA-VP-2/10	ASK-VP-3/401	ESC2/P430	STD-VP-2/62	
<i>Ardipithecus ramidus</i>	27	ARA-VP-1/1	ARA-VP-6/500	ARA-VP-6/1	GWM5M/P55	KUS-VP-2/154
		ARA-VP-1/128	ARA-VP-1/300	ARA-VP-6/500	GWM5SW/P56	SAG-VP-7/118
		ARA-VP-1/1814	ARA-VP-1/3288	ARA-VP-6/502	GWM9N/P50	SAG-VP-7/225
		ARA-VP-1/1818	ARA-VP-1/400	ARA-VP-6/514	GWM9N/P51	
		ARA-VP-1/1875	ARA-VP-1/401	GWM16/P10	KUS-VP-2/100	
		ARA-VP-1/200	ARA-VP-1/703	GWM3W/P185	KUS-VP-2/102	
<i>Australopithecus anamensis</i>	36	ARA-VP-14/1	KNM-ER 20432	KNM-ER 35233	KNM-KP 30498	KNM-KP 47953
		ASI-VP-2/2	KNM-ER 22683	KNM-ER 35236	KNM-KP 30500	KNM-KP 47954
		ASI-VP-2/334	KNM-ER 30200	KNM-ER 35238	KNM-KP 31712	KNM-KP 49388
		ASI-VP-5/1	KNM-ER 30201	KNM-ER 7727	KNM-KP 31717	KNM-KP 52120
		ASI-VP-6/186	KNM-ER 30745	KNM-KP 29281	KNM-KP 31723	
		KNM-ER 20420	KNM-ER 35228	KNM-KP 29283	KNM-KP 34725	
		KNM-ER 20421	KNM-ER 35231	KNM-KP 29286	KNM-KP 35852	
		KNM-ER 20428	KNM-ER 35232	KNM-KP 29287	KNM-KP 47951	
<i>Australopithecus</i> Late Pliocene (exclusive of <i>Au. deyiremeda</i>)	110	AL 582-1	AL 333-1	AL 438-2	Garusi II	LH-14
		AL 128-23	AL 333-10	AL 440-1	KER-VP-1/185	LH-15
		AL 145-35	AL 333-2	AL 443-1	KNM-WT 16003	LH-16
		AL 161-40	AL 3332-32,60	AL 444-2	KNM-WT 16006	LH-17
		AL 188-1	AL 333-44	AL 462-7	KNM-WT 38337	LH-19
		AL 198-1	AL 333-74	AL 486-1	KNM-WT 38350	LH-2
		AL 199-1	AL 333-86	AL 582-1	KNM-WT 38358	LH-21
		AL 200-1	AL 333w-1	AL 620-1	KNM-WT 38359	LH-26
		AL 207-13	AL 333w-12	AL 651-1	KNM-WT 40000	LH-29
		AL 207-17	AL 333w-27	AL 770-1a	KNM-WT 8556	LH-3
		AL 225-8	AL 333w-32,60	AMA-VP-2/30	KNM-WT 8557	LH-31
		AL 228-2	AL 333w-42	ARI-VP-1/215	KSA-VP-2/193	LH-4
		AL 241-14	AL 333w-46	ARI-VP-1/484	KT 12/H1	LH-5
		AL 266-1	AL 333w-48	ARI-VP-1/520	LDD-VP-1/167	LH-6
		AL 277-1	AL 333w-57	ARI-VP-1/90	LDD-VP-1/248	LH-8
		AL 288-1	AL 333w-58	ARI-VP-3/176	LDD-VP-1/26	MAK-VP-1/12
		AL 299-1	AL 333w-59	ARI-VP-3/248	LDD-VP-1/406	MAK-VP-1/2
		AL 300-7	AL 333x-1	ARI-VP-3/249	LDD-VP-1/672	MAK-VP-1/4
		AL 311-1	AL 400-1a	ARI-VP-3/80	LDD-VP-1/732	MSD-VP-1/53
		AL 315-22	AL 417-1	BDU-VP-1/24	LDD-VP-1/775	MSD-VP-5/16
		AL 330-5	AL 423-1	BDU-VP-1/64	LDD-VP-1065	MSD-VP-5/50
		AL 330-7	AL 437-1	Garusi I	LH-11	NFR-VP-1/29
<i>Australopithecus deyiremeda</i>	6	BRT-VP-1/120	BRT-VP-2/89	BRT-VP-3/14		
		BRT-VP-1/2	BRT-VP-3/1	BRT-VP-3/37		

TABLE 3 (following). – List of the 359 comparative specimens by taxonomic category.

Taxa	N	Specimen inventory numbers			
<i>Australopithecus garhi</i>	1	BOU-VP-12/130			
<i>Homo</i> early eastern Africa	38	AL 666-1	KNM-ER 1813	KNM-ER 808	OH 41
		KNM-ER 1462	KNM-ER 1814	OH 13	OH 44
		KNM-ER 1482	KNM-ER 2597	OH 15	OH 45
		KNM-ER 1502	KNM-ER 2601	OH 16	OH 6
		KNM-ER 1506	KNM-ER 3953	OH 21	OH 60
		KNM-ER 1508	KNM-ER 42703	OH 24	OH 65
		KNM-ER 1590	KNM-ER 60000	OH 27	OH 7
		KNM-ER 1801	KNM-ER 62000	OH 37	UR 501
		KNM-ER 1802	KNM-ER 64060	OH 39	
		KNM-ER 1805	KNM-ER 807	OH 4	
<i>Homo erectus</i>	71	Arago 13	KNM-ER 3733	S 7-31	Sangiran 4
		Bk 7905	KNM-ER 730	S 7-32	Sangiran 5
		Bpg 2001.04	KNM-ER 806	S 7-35	Sangiran 6
		D211	KNM-ER 820	S 7-37	Sangiran 8
		D2282	KNM-ER 992	S 7-38	Sangiran 9
		D2600	KNM-WT 15000	S 7-3	Sb 8103
		D2700	MA 93	S 7-40	Sh.y.003
		D2710	Mauer	S 7-53	Sh.y.007
		D2711	Ng 8503	S 7-58	Sh.y.0071
		D2735	Njg 2005.05	S 7-8	Sh.y.008
		KGA10-1	OH 22	S 7-9	Sh.y.072
		KGA11-350	PA636	Sangiran 1	Thomas Quarry 1
		KGA4-14	PA637	Sangiran 15	Tighenif 1
		KNM-BK 67	Pithecanthropus IV	Sangiran 16	Tighenif 2
		KNM-BK 8518	S 7-10	Sangiran 17	Tighenif 3
		KNM-ER 1507	S 7-27	Sangiran 21	Zhoukoudian G1-6
		KNM-ER 1808	S 7-29	Sangiran 22	Zhoukoudian G1-7
		KNM-ER 1812	S 7-30	Sangiran 27	
<i>Paranthropus aethiopicus</i>	14	F 22-1a	L 338/X-40	L 62-17	OMO 18-1968-34
		KNM-WT 17000	L 398-120	L 860-2	OMO 33-1969-9
		L 157-35	L 51-79	OMO 18-1968-31	OMO 33-1971-508
		L 338/X-39	L 55-33		
<i>Paranthropus boisei</i>	47	HCRP RC 911	KNM-ER 15930	KNM-ER 5877	KNM-WT 17400
		KGA10-1720	KNM-ER 15940	KNM-ER 6080	KNM-WT 37747
		KGA10-506	KNM-ER 15950	KNM-ER 6128	KNM-WT 37748
		KGA10-525	KNM-ER 1804	KNM-ER 6128	OH 26
		KGA10-570	KNM-ER 1816	KNM-ER 729	OH 30
		KMN-ER 729	KNM-ER 1820	KNM-ER 733	OH 38
		KNM-CH 1	KNM-ER 25520	KNM-ER 801	OH 5
		KNM-ER 1171	KNM-ER 3229	KNM-ER 802	OH 66
		KNM-ER 1467	KNM-ER 3230	KNM-ER 810	OH 74
		KNM-ER 1477	KNM-ER 3885	KNM-ER 818	OH 80-2
		KNM-ER 1480	KNM-ER 3890	KNM-WT 16005	Peninj 1 (NMT-W64-160)
		KNM-ER 1509	KNM-ER 404	KNM-WT 17396	

TABLE 4. – Position and counts of the 809 teeth represented by the 359 comparative specimens¹.

Taxon		<i>Ar. kadabba</i>	<i>Ar. ramidus</i>	<i>Au. anamensis</i>	<i>Au. deyiremeda</i>	<i>Au. LP</i>	<i>Au. garhi</i>	<i>H. EEA</i>	<i>H. erectus</i>	<i>P. aethiopicus</i>	<i>P. boisei</i>
Total		9	68	63	13	239	5	117	182	17	96
maxillary	P ³	1	7	6	1	12	1	12	17	0	7
	P ⁴	0	8	3	3	15	1	12	14	1	5
	M ¹	4	9	9	1	15	1	17	17	0	8
	M ²	0	8	9	1	16	1	11	12	0	6
	M ³	2	5	8	0	16	1	10	7	0	4
mandibular	P ₃	-	-	-	1	31	0	8	16	3	7
	P ₄	2	8	7	3	37	0	9	19	5	12
	M ₁	0	9	7	1	34	0	14	26	1	12
	M ₂	0	7	6	1	35	0	12	31	4	15
	M ₃	0	7	8	1	28	0	12	23	3	20

¹ We did not include measurements for the mandibular third premolars of *Ardipithecus* or *Au. anamensis* because basic mesiodistal and buccolingual dimensions of their ancestral morphology are not directly comparable with the mesiodistal and buccolingual dimensions of the more derived morphology of the other taxa.

METHODS

For this analysis, we focused on the outer enamel surface size and shape of the postcanine tooth crowns. Analyses of the enamel dentin junction will be conducted in a subsequent study.

We employed a four-step approach to obtain the most-likely taxonomic identifications for the postcanine teeth in the IORE and OGRE collections. Three subsets of our study are quantitative: 1) univariate and ANOVA investigation of the linear metrics of the comparative dataset to provide context for the individual Omo specimens; 2) a discriminant function analysis of linear metrics for the Omo teeth (with unknown taxonomy) against a comparative dataset of teeth with taxonomic status assumed to be reliable (i.e., because they are within jaws and/or have consensus in the literature) to estimate the most-likely genus and species identifications for each tooth; 3) hierarchical cluster analyses of discrete morphological scores and molar cusp areas of the Omo assemblage to identify whether or not taxonomic clusters exist within the assemblage. The fourth, and last component of our study was the final determination of taxonomic identification for each tooth based on our qualitative description combined with results from

the three quantitative approaches. In Table 2, we indicate which teeth from the Omo were included in each of the quantitative approaches, and also report the conclusion reached through the fourth component of the study.

DATA COLLECTION

All data for the Omo teeth used in this study derive from the external morphology of the outer enamel surface. Data were collected from the original fossils, photographs of the original fossils, and/or from high-resolution plaster replicas of the fossils. The plaster study casts are held at the University of Poitiers and CENIEH. The original fossils belong to the collections preserved by the Ethiopian Heritage Authority/National Museum of Ethiopia in Addis Ababa.

Linear metrics

The maximum mesiodistal (MD) lengths and maximum buccolingual (BL) breadths for the Omo teeth were measured by L.J.H. using Mitutoyo calipers from the original fossils at the Ethiopian Heritage Authority in Addis Ababa. For molars, we report and analyze the BL breadth across the mesial cusps. Each measurement was collected three times, the average used as the data point. If a portion of a crown was broken or heavily worn, compromising our ability to determine the actual dimension of the crown, we did not record that measurement. For the MD dimensions, many of the crowns have interstitial wear. Our MD dimensions report the actual length of the crown as it currently is; we did not attempt to correct for the wear (see Section 3.2 for discussion). Linear metrics were analyzed against the comparative dataset to identify the most-likely taxonomic assignment. See Appendix 1 for these linear measurements; these data are also freely available at (*reference to Data Dryad DOI once uploaded*).

Molar cusp areas

Cusp area data were collected by I.T. from the photographs of the original specimens taken by F.G. When photographed, each molar was oriented so that the occlusal crown area was maximized (e.g., Grine *et al.* 2009). The orientation that best captured the occlusal view horizontal to the camera lens was used for measuring cusp areas.

The occlusal images of complete molars were analyzed using ImageJ software (Schindelin *et al.* 2015). Individual images were uploaded into ImageJ and calibrated using the set scale function by measuring the millimeters scale bar in each image. Outlines were drawn separately around each cusp following Brophy

et al. (2021) and Bailey *et al.* (2004). Similar methodology has been employed in a variety of samples (e.g., Martín-Albaladejo *et al.* 2017; Quam *et al.* 2009; Suwa *et al.* 1994).

The occlusal areas of the ‘main’ cusps were calculated (paracone, protocone, metacone, and hypocone for the upper molars, and the protoconid, metaconid, hypoconid, entoconid and hypoconulid for the lower molars; see Fig. 3). All cusp areas were then summed to obtain a total crown area (following Bailey *et al.* 2004; Wood *et al.* 1983). If required, corrections of the cusp outlines were made to account for loss of tissue, especially in interproximal regions. This reconstruction was performed in ImageJ following Bailey (2004). If accessory cusps were present, they were divided equally between the adjacent ‘main’ cusps following Wood *et al.* (1983). Each cusp was measured to the nearest 1 mm², following Kondo and Townsend (2006).

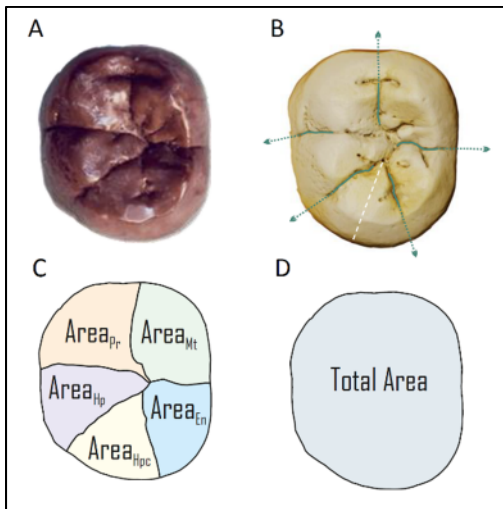


FIG. 3. – Methodology for calculating cusp area. This illustration shows a lower molar (L1/nn-10010b): **A**, a scaled occlusal image; **B**, occlusal surface split into the separate cusps, following major fissures; **C**, area of each cusp calculated in ImageJ (Pr: Protoconid; Mt: Metaconid; Hp: Hypoconid; HPC: Hypoconulid; En: Entoconid); **D**, all cusps combined to get a total occlusal area. Note, two separate analysis were performed, one with all cusps included and one with only the four ‘main’ cusps. For this later analysis, additional cusps are split between the two adjacent ‘main’ cusps. In this case, the HPC would be split equally between the Hp and En (white dashed line in B). See section Molar cusp areas for details.

Individual cusp areas were defined by following the main fissures of the occlusal surface. Crowns in which occlusal fissures were completely removed through wear were not recorded, following Grine *et al.* (2009). However, if substantial areas of the main fissures were eroded by wear but the course of each could be estimated, we extrapolated the course based on the preserved part of the fissures (following Gómez-Robles *et al.* 2011). Relative cusp areas were calculated by dividing the absolute area of each cusp by the total crown area.

The molar cusp area analysis used a total sample of 33 mandibular molars and 16 maxillary molars. This sample includes only specimens from the Omo (i.e., no comparative material). We included in this sample those additional Omo specimens that were attributed to *P. aethiopicus* and used in the comparative dataset for the linear metric analyses (see Section 3.1 for details). See Table 2 for a list of specimens and the published DataDryad dataset for measurements (*reference to Data Dryad DOI once uploaded*).

Morphological scores

Many morphological features of crown shape can be scored using a modified version of the Arizona State University Dental Anthropology System (ASUDAS). There is an extensive literature demonstrating that these morphological traits typically have high heritability and are a reliable proxy for genetic relationships between populations (Hlusko 2003; Scott *et al.* 2018; Martínón-Torres *et al.* 2007; Ricaut *et al.* 2010; Rizk *et al.* 2008). Many of these traits can also be recorded even in substantially worn teeth, and show low variation between the sexes (e.g., Pilloud & Scott 2020).

Originally created as a standardized way for scoring key morphological features of the human permanent dentition, the ASUDAS methods have more recently been applied to the hominin fossil record (e.g., Irish and Guatelli-Steinberg 2003; Martínón-Torres *et al.* 2012; Louail & Prat 2018; Bermúdez de Castro *et al.* 2019; Irish *et al.* 2013; Irish *et al.* 2018), although often with varying recording criteria and dichotomization (i.e., recording the same features but using slightly different methods/criteria). Recording criteria for certain traits have been slightly altered to better record the range of variation in fossil hominins, or new traits have been added for particular teeth (e.g., Martínón-Torres *et al.* 2012; Irish *et al.* 2018). We follow the methodology outlined in Martínón-Torres *et al.* (2012), in which a subset of ASUDAS traits (including some altered trait categories) are recorded for each specimen, with other ASUDAS traits from Turner *et al.* (1991) added for particular features/teeth. For this study, we recorded 37 traits that are described in Table 5. Specimens were scored twice by the same author (M.M.P.), first using the high-resolution casts and then from photographs of the original specimens.

In total, 14 maxillary premolars, 18 mandibular premolars, 23 maxillary molars, and 39 mandibular molars were included in the morphological analysis (see Table 2). We only included teeth in the morphological analysis if they had all traits scored. Note that one tooth (OMO 75/i-1970-1255) had all traits scored but was not included in the LD analysis because we could not accurately measure both the MD and BL dimensions (Table 2). See the published DataDryad dataset for scores (*reference to Data Dryad DOI once uploaded*).

TABLE 5. – The 37 premolar and molar morphological traits scored.

Maxillary premolars		
PREMOLAR DISTAL ACCESSORY RIDGE		ridge development between the cusp tip and the distolingual marginal ridge in the buccal cusp
PREMOLAR MESIAL ACCESSORY RIDGE		ridge development between the cusp tip and the mesiolingual marginal ridge in the buccal cusp
TRANSVERSE CREST OF PREMOLARS		expression of a transverse crest connecting the main cusps of the premolars
DISTO-BUCCAL CUSPLET		presence of a secondary buccal cusp detached from the main buccal cusp
DISTOSAGITTAL RIDGE		ridge from the apex of the buccal cusp to the distal occlusal border at or near the sagittal sulcus
MESIAL AND DISTAL ACCESSORY CUSPS		small accessory cusps at the mesial and/or distal ends of the sagittal grooves
TRICUSPED PREMOLARS		additional distolingual cusp
BUCCAL ESSENTIAL CREST OR RIDGE		degree of expression and possible bifurcation
LINGUAL ESSENTIAL CREST OR RIDGE		same scoring as the buccal essential crest
Mandibular premolars		
PREMOLAR DISTAL ACCESSORY RIDGE		ridge development between the cusp? apex and the distolingual marginal ridge in the buccal cusp
PREMOLAR MESIAL ACCESSORY RIDGE		ridge development between the cusp? apex and the mesiolingual marginal ridge in the buccal cusp
TRANSVERSE CREST OF PREMOLARS		expression of a transverse crest connecting the main cusps of the premolars
DISTO-BUCCAL CUSPLET		presence of a secondary buccal cusp detached from the main buccal cusp
LINGUAL CUSP VARIATION OF THE LOWER PREMOLARS		refers to the number of lingual cusps, including main and accessory lingual cusps. frequently, accessory cusps adopt the shape of tubercles without a clear tip and are difficult to differentiate from enamel wrinkles
MESIOLINGUAL GROOVE		groove on the mesiolingual aspect of the tooth
METACONID PLACEMENT		position of the metaconid relative to the protoconid
CROWN ASYMMETRY		shape of the lingual contour of the tooth in occlusal view

TABLE 5 (following). – The 37 premolar and molar morphological traits scored.

Maxillary Molars	
METACONE	refers to the expression of this cusp
HYPOCONE	refers to the expression of this cusp
CUSP 5 (METAONULE)	presence of a secondary distal cusp in addition to cusp 5
CRISTA OBLIQUA	expression of an enamel crest connecting the protocone and the metacone
TRANSVERSE CREST	crest connecting the mesial aspect of the protocone and the paracone
CARABELLI'S CUSP	tubercle of various degrees of expression on the lingual surface of the protocone
PARASTYLE	tubercle of various degrees of expression on the buccal surface of the paracone
MESIAL MARGINAL ACCESSORY TUBERCLES	presence of tubercles in the mesial marginal ridge of upper molars
DISTAL FOVEA	development of a triangular depression mesial to the distal marginal ridge
Mandibular Molars	
ANTERIOR FOVEA	fovea or groove on the anterior occlusal surface, distal to the mesial marginal ridge
MIDDLE TRIGONID CREST	crest connecting the mesial aspects of the protoconid and the metaconid
DISTAL TRIGONID CREST	crest connecting the distal aspect of the protoconid and the metaconid
DEFLECTING WRINKLE	the essential crest of the paraconid is distally deflected
HYPOCONULID SIZE	refers to the size of the hypoconulid or the cusp 5
C6 (ENTOCONULID OR TUBERCULUM SEXTUM)	the presence of a hypoconulid is not necessarily required to record a C6. When there is one single distal cusp and it occupies a lingual position, we consider it a C6
DOUBLE CUSP 6	presence of a secondary distal cusp between cusps 5 and 6
C7 (METAONULID)	accessory cusp between the metaconid and the entoconid
GROOVE PATTERN	type of groove pattern
PROTOSTYLID	tubercle of various degrees of expression on the buccal surface of the lower molars
MESIAL MARGINAL RIDGE	development of the mesial marginal ridge

Morphological descriptions

Measurement and scoring of morphology do not completely capture the anatomical variation of hominin teeth. Therefore, descriptions of crowns (written by M.M.P. and L.J.H.) are also included in our analysis. Our descriptions focus on characteristics that have previously been considered important in differentiating between hominin taxa, as detailed below. In addition to the morphological scores described in the previous section, we also turned to the dental characters used in phylogenetic systematics to identify tooth characteristics considered taxonomically diagnostic. For this, we rely primarily on Strait and Grine (2004) who provide a detailed consideration of characters employed in previous cladistic analyses. Of the 198 characters they deem reliable, 28 are specific to the dentition. However, only ten characters are applicable to isolated permanent postcanine teeth. These ten characters are listed in Table 6 along with the character states for each of the taxa included in our comparative sample (as determined by Strait and Grine 2004). We applied our taxonomic terminology to the data presented by Strait and Grine (2004), and therefore combine *Sahelanthropus tchadensis* with *Ar. ramidus*,

and *Kenyanthropus platyops* and *Au. bahrelghazali* with *Au. afarensis* into *Australopithecus* LP. We pooled *Homo habilis* and *Homo rudolfensis* into *Homo* EEA. And lastly, we categorize *H. ergaster* as *H. erectus*.

Size of the teeth: A review of Table 6 shows that these characters are moderately informative for our study. The first character describes premolar size, showing that *Au. garhi* and *Paranthropus* spp. have large premolars and the other hominins have small premolars. The second character captures the size of the molars, and again, shows that *P. aethiopicus* and *P. boisei* have the largest molars, molars of *P. robustus* and *Au. garhi* are the next largest, molars of *Au. anamensis*, some *Au. afarensis*, and early *Homo* are somewhat large, and *Ar. ramidus*, *H. erectus* and *H. sapiens* have relatively small molars. Enamel is also relatively thick in *Paranthropus* compared to *Australopithecus* and *Homo*.

Molars: Aside from size, the general molar shape of *Paranthropus* differs from other hominin taxa in having a more bulbous or bulging appearance that can either be described in terms of the cross-sectional shape or in terms of the occlusal shape. For example, Strait and Grine (2004) include a character that reflects whether or not the buccal cusps of mandibular molars are more buccally or lingually positioned, and vice versa for the maxillary molars. Cusps shifted away from the cervical margin are characteristic of *Paranthropus* (character 3, Table 6). When observed in occlusal view, the occlusal central basin, defined as the region between the cusp tips, appears more closed in *Paranthropus* and more open in other hominins. This same feature can be described in cross-section as well. For example, Tobias (1967) described the shape of the crown sides, noting that the buccal and lingual surfaces of the premolars and molars of *Zinjanthropus boisei* (referred to herein as *P. boisei*) “swell out” such that the maximum bulge of the enamel extends past the cervix of the crown by as much as 3.5 mm (1967: 179-192). There have been some efforts to quantify this bulging feature using geometric morphometrics (e.g., Tobias 1967; Wood *et al.* 1983; Hlusko 2002).

There are a few other mandibular molar features that we include in our consideration. Villmoare *et al.* (2015) noted that enlargement of lower molar entoconids is typical of *Paranthropus*, which is one of the characters that they argue aligns LD 350-1 (a 2.8 Ma specimen from the Afar, Ethiopia) with *Homo*. Suwa *et al.* (1996) reported that robust hominin molars typically have a C6 to hypoconulid area ratio that approaches 1, and when the teeth are worn, they have flat occlusal wear. In contrast, non-robust hominins tend to have a small or absent C6 on the M₂, typically lack C6 but do have a C7 (Wood & Abbott 1983), and have more asymmetrical wear on the occlusal surface.

Maxillary premolars: Strait and Grine (2004) include a trait that scores the relative size of the P³ paracone and protocone (character 6, Table 6). They find that *Ar. ramidus* differs from the other hominins in having a paracone larger than the protocone, whereas all other hominins have cusps of equivalent sizes.

Asfaw *et al.* (1999) note that *Au. afarensis* has a more asymmetrical P³ occlusal outline, whereas *Au. garhi*, early *Homo*, and *Paranthropus* have a more oval occlusal outline. Additionally, Asfaw *et al.* (1999) note that variation in the mesiobuccal aspect of the P³ has taxonomic valence, as it is frequently extended in *Au. afarensis*, and absent or rare in *Homo* and *Paranthropus*. Premolar molarization is also often referred to in hominin taxonomy, though this can be a difficult trait to differentiate into categories given how continuously variable it is.

Mandibular premolars: In their detailed analysis of the Omo Shungura mandibular dentitions, Suwa *et al.* (1996) conducted a multidimensional analysis of mandibular premolar shape that differentiated robust from non-robust taxa. Translating their analysis into a morphological description, the mandibular premolars of robust hominins have more mesially positioned cusps and an extended/enlarged talonid compared to non-robust taxa. This pattern is especially pronounced in P₃s, but is also reflected in P₄s (Suwa *et al.* 1996). Strait and Grine (2004) noted that *Ar. ramidus* and *Au. anamensis* are differentiated from other hominins in their lack of a P₃ metaconid, with *Au. afarensis* being intermediate in expression (character 4, Table 6). Additionally, the P₃ of *Ar. ramidus* and *Au. anamensis* has a mesiobuccal protrusion of the crown base, differentiating them from *Paranthropus* and *Homo*, with *Au. afarensis* having variable expression. This extension of the talonid is part of the molarization of the mandibular premolars that we also consider. Strait and Grine's character 4 (in our Table 6) captures this feature to a certain degree as well (2004).

TABLE 6. – Character states used in cladistic analyses (Strait & Grine 2004) that are applicable to isolated permanent postcanine teeth.

Characters	<i>Ar.</i> <i>ramidus</i>	<i>Au.</i> <i>anamensis</i>	<i>Au.</i> LP	<i>Au.</i> <i>garhi</i>	<i>P.</i> <i>aethiopicus</i>	<i>P.</i> <i>robustus</i>	<i>P.</i> <i>boisei</i>	<i>H.</i> EEA	<i>H.</i> <i>erectus</i>	<i>H.</i> <i>sapiens</i>
1. Premolar crown area	1	1	1	4	4	3	5	1 or 2	1	0
2. Molar crown area	0	1	0 or 1	2	3	2	3	1 or 2	0	0
3. Positions of buccal and lingual cusps relative to crown margin	1 or 2	2	1	1	4	4	4	1	1	1
4. Frequency of well developed P ₃ metaconid	0	0	1	?	2	2	2	2	2	2
5. Mesio Buccal protrusion of P ₃ crown base	1	1	2	3	3	3	3	3	3	3
6. Basal area of paracone of p ₃	1	2	2	2	2	2	2	2	2	2
7. Relative enamel thickness	0	1	1	1	2	2	2	1	1	1
8. Molar cingulum	3	3	3	3	3	3	3	3	3	3
9. Protocristid groove of lower molars	?	?	?	?	?	?	?	?	?	0
10. Lingual marginal ridges of molars	?	?	?	?	?	?	?	?	?	1

Character 1: 1 = small; 5 = largest

Character 2: 0 = smallest; 4 = large

Character 3 (stated for mandibular teeth; reverse for maxillary teeth): 1 = Lingual cusps approximate margin; buccal cusps slightly lingual to margin; 2 = Lingual cusps approximate margin; buccal cusps moderately lingual to margin; 4 = Lingual cusps moderately buccal to margin; buccal cusps strongly lingual to margin

Character 4: 0 = absent; 1 = infrequent; 2 = frequent

Character 5: 1 = moderate; 2 = variable; 3 = weak or absent

Character 6: 1 = paracone larger than protocone; 2 = paracone equals protocones

Character 7: 0 = thin; 1 = thick; 2 = hyperthick

Character 8: 3 = fragmented or absent

Character 9: 0 = prominent

Character 10: 1 = more prominent

ANALYTICAL METHODS

We employed three analyses of quantitative data. First, for the comparative data we calculated the univariate statistics for the MD and BL dimensions, as well as MDxBL (2-dimensional crown size) and MD/BL (a ratio that captures the crown shape from occlusal view, also called the ‘shape ratio’). We then ran an analysis of variance (ANOVA) for these four parameters from the comparative dataset. Our second analytical approach was the development of the linear discriminant classification method that was based on these same four parameters (MD, BL, MDxBL, and MD/BL) using the comparative dataset to then classify the Omo specimens. Third, we conducted a hierarchical clustering analysis for morphological scores and cusp areas for the Omo specimens.

Univariate and Analysis of Variance (ANOVA) of Linear Measurements

The first step in our study is to provide perspective on the means and distributions of the linear measurements for our comparative samples. We compared means between genera and between species using the Kruskal-Wallis test, a non-parametric ANOVA approach. For this ANOVA, we included a Dunn’s post hoc test for pairwise comparisons with a Bonferroni correction, given the large number of analyses. In order to identify taxa with unequal variances, we ran a Levene’s test for both the genus and the species analyses. All analyses were performed by M.F.B. using the packages `car` (v3.1.2, Fox and Weisberg 2019), `FSA` (v0.9.5, Ogle *et al.* 2023), and `dplyr` (v1.1.4, Wickham *et al.* 2023) in the R statistical environment (v4.3.2, R Core Team 2023).

Linear Discriminant Analysis (LDA) of Linear Measurements

Linear discriminant analysis (LDA) is a classification method based on linear combinations of the predictors that classify cases into one of a fixed number of possibilities (Faraway 2016). Based on our relatively large comparative dataset of mesiodistal (MD) and the mesial buccolingual (BL) diameters of all postcanine tooth types, along with their estimated areas (MDxBL) and proportions (MD/BL), different linear functions were created to predict the taxon (genus or species) to which each tooth from the Omo sample belongs based on the observations from the comparative sample. The first two variables are measured in millimeters, the third is measured in square millimeters and the fourth is adimensional.

We used the function `lda()` from the package *MASS* (Venables and Ripley 2002) in R (v4.2.2 R Core Team, 2022) to run the discriminant functions. We created linear discriminant functions (LDFs) to predict species attributions and another set of LDFs to predict generic attributions. The species output can be any of ten hominin taxa: two species of *Ardipithecus* (*Ar. kadabba*, *Ar. ramidus*), four taxa of *Australopithecus*

(*Australopithecus* LP, *Au. anamensis*, *Au. deyiremeda* and *Au. garhi*), two of *Paranthropus* (*P. aethiopicus* and *P. boisei*) and two of *Homo* (*Homo* EEA and *Homo erectus*). The genus output can be one of four options: *Ardipithecus*, *Australopithecus*, *Paranthropus* and *Homo*. The four variables (MD, BL, MDxBL, MD/BL) were scaled before running the discriminant functions with the function `scale()` of the base package in R (R Core Team 2022) in order to treat them equally, so they all have the same weight in the analysis.

For each Omo tooth, the LDA output provides the probability of it belonging to each of the species/genera. The species/genus with the highest probability was selected as the most likely option. The plots representing linear discriminant functions 1 and 2 for each tooth type were generated by using the packages `ggplot` (Wickham, 2016) and `ggrepel` (Slowikowski 2023) in R.

Confusion matrices were used to evaluate the performance of the linear discriminant functions when predicting genus and species attributions for the Omo teeth. For this purpose, two R packages were used: `gmodels` (Warnes *et al.*, 2022) and `cvms` (Olsen and Zachariae 2019). The LDA was designed and run by M.M-M.

Hierarchical Clustering

Clustering is a data mining method for discovering patterns among multidimensional data, which allows for the identification of groups (or clusters) of similar objects within a dataset (Kassambara 2017). Unsupervised clustering was selected because it is not guided by a priori ideas of which teeth belong in which clusters. The hierarchical cluster analysis (HCA) was employed in two cases: (1) to cluster morphological traits of the premolars and molars, and (2) to cluster cusp areas of molars. All hierarchical clustering analyses were performed by M.M-M.

Morphological scores

The morphological scores of the teeth can be treated as nominal/categorical data. Therefore, the R package `nomclust` was used as this package was specifically developed to run HCAs of objects characterized by nominal variables (Sulc, Cibulkova, and Rezankova 2022; Sulc *et al.* 2023). Internally, this package converts the original matrix of scores into a boolean matrix of scores with the one-hot encoding algorithm.

The Omo teeth used in this analysis were separated by tooth type and position: upper and lower premolars and molars. The default settings of the `nomclust()` function when running HCAs are the linkage measure and the average method. The output of the `nomclust()` function serves as an input for the

visualization functions `dend.plot()` and `eval.plot()`. `eval.plot()` was used to calculate the optimal number of clusters in each HCA by including all criteria, whereas `dend.plot()` was used to plot the HCA from `nomclust()` and identify the optimal number of clusters from `eval.plot()`.

Molar cusp areas

Cusp areas of the molars are numerical data, therefore, the HCA we applied was slightly different than the one we used for the morphological scores. The data were scaled with `scale()` as not only the areas in square millimeters were used but also their relative proportion in the total area of the occlusal surface. By scaling the data, all the variables are treated equally in the analysis, avoiding bias.

HCA was run by computing first the distance matrix with the Euclidean distance measure using the function `dist()` of the `stats` package (R Core Team 2022). Later, the distance matrices were included in the `hclust()` function of the same package to run the HCA with the agglomeration method `ward.D2`. Both the Euclidean distance measure and the `ward.D2` agglomeration method are fitted to work with numerical data (Modesto Mata 2020).

The HCA dendrograms were obtained by running the function `fviz_dend()` of the package `factoextra` (Kassambara and Mundt, 2020). The optimal number of clusters identified were automatically calculated by using the silhouette method provided in the package.

QUALITATIVE ASSESSMENT OF TAXONOMY

For the fourth step in our analysis, we returned to the replicas and photographs of each of the Omo dental specimens. Alongside the LD results, the morphological scores, and the qualitative descriptions, we added a subjective component to our taxonomic identifications by considering the weight of the evidence for the taxonomic assignment. For our final taxonomic designation, we took a conservative approach given that many diagnostic dental characteristics require fairly complete dentitions and that there is considerable overlap in tooth size and shape across hominin taxa.

ABBREVIATIONS AND DEFINITIONS

OGRE	Omo Group Research Expedition
IORE	International Omo Research Expedition
<i>Australopithecus</i> LP	<i>Australopithecus</i> Late Pliocene
<i>Homo</i> EEA	<i>Homo</i> early eastern Africa
MD	mesiodistal dimension of a tooth crown
BL	buccolingual dimension of a tooth crown
ASUDAS	Arizona State University Dental Anthropology System

99	LDA	linear discriminant function analysis
100	LD1, LD2	First and second linear discriminant function, respectively
101	HCA	hierarchical clustering analysis
102	Stdv	standard deviation
103	Hominin	<i>Homo sapiens</i> and all extinct genera and species on the human side of the family
104		tree since we last shared a common ancestor with chimpanzees. This terminology
105		reflects the phylogenetic systematics approach to taxonomy and not a biological
106		approach
107	Dental notations	P ³ , upper third premolar; P ₃ , lower third premolar; P3, maxillary and mandibular
108		third premolars; M, maxillary and mandibular molars, dP, decidual premolars.
109		

111 RESULTS

113 We first present an analysis of the linear metric data for the comparative dataset, as this provides
 114 information on how taxonomically informative isolated teeth can be. We use these results to develop the
 115 taxonomic categories that are possible to identify within the Omo sample. We then present the
 116 quantitative analyses for the Omo sample, followed by the qualitative descriptions and quantitative
 117 consideration of each Omo tooth.

118 The linear metrics, 2-dimensional cusp areas, and morphological trait scores for the Omo teeth
 119 included in this study (Table 2) are published on Data Dryad (*reference DATA DRYAD DOI*).

121 UNIVARIATE STATISTICS AND COMPARISON OF VARIANCES FOR THE LINEAR METRICS OF THE COMPARATIVE DATASET

122 The means and variances for the linear metrics from the comparative dataset for genera are presented in
 123 Supplemental Table S2. The univariate statistics for the mandibular and maxillary species means are
 124 presented in Supplemental Tables S3 and S4, respectively. We present the species data in box and whisker
 125 plots by tooth in Figs. 4 through 13.

126 Taxa with unequal variances, as determined through the Levene's test, are indicated with asterisks in
 127 Supplemental Tables 2, 3, and 4. For the genus level analyses, Levene's test indicates only *Homo* has a
 128 variance that differs significantly from the other genera for measurements of P₄, M₁, M₂, M₃, M¹, and for
 129 the MDxBL of M². For the species analyses, the Levene's test only highlights *P. aethiopicus* as having
 130 unequal variances, involving the P₄, M₂, M₃, and P³, likely the result of the very small sample sizes for this
 131 species (Table 4). *Homo erectus* is also identified as having unequal variance for the P³ shape index
 132 (MD/BL) (Supplemental Table S4).

COMPARISON OF MEANS BETWEEN GENERA AND SPECIES IN THE COMPARATIVE DATASET

Results from the Kruskal-Wallis non-parametric one-way ANOVA, used to test whether or not two means are from the same distribution (population), are presented in Supplemental Tables S5, S6, and S7. We report only the Bonferroni adjusted p-values. The results for the genus-by-genus analyses are reported in Supplemental Table S5. The mandibular species comparisons are reported in Supplemental Table S6, and the maxillary species results are presented in Supplemental Table S7.

Genus level analyses: Size measurements (MD, BL, and MDxBL)

This section discusses the results presented in Supplemental Table S5, focusing only on the size dimensions. *Paranthropus* is statistically different from *Ardipithecus*, *Australopithecus*, and *Homo* for all the mandibular teeth. While *Paranthropus* is significantly different from *Ardipithecus* and *Homo* for all maxillary teeth, it is not statistically different from the size of *Australopithecus* teeth for P⁴ and M³. This result for the maxillary teeth is likely driven by the inclusion of *Au. garhi*, for which we only have the maxillary dentition.

Australopithecus and *Homo* are only statistically different in the MD dimension of P₄, the BL dimension of M₃, and the BL and MDxBL of the P⁴. For all other linear size dimensions, *Australopithecus* and *Homo* are statistically indistinguishable.

Ardipithecus is statistically different from *Australopithecus* in all mandibular linear size dimensions except for the MD of M₂. For the maxillary dentition, *Ardipithecus* is different from *Australopithecus* for all linear size dimensions except for the BL of P³, and for the MD and BL of M², and the BL of M³, and consequently, the MDxBL for both of these molars as well. For the maxillary and mandibular teeth, the linear metrics of *Ardipithecus* and *Homo* are often similar, only being statistically distinguishable for the M₁ and M¹.

Genus level analyses: Shape (MD/BL)

This section also discusses the results presented in Supplemental Table S5, focusing only on the shape index (shape ratio). The shape ratios of the maxillary and mandibular premolars of *Paranthropus* are not statistically distinguishable from any of the other genera, indicating that it is the size of the premolars and not the general shape of these teeth that make them distinguishable from the non-robust genera (which is at odds with the results of Wood & Engleman (1983) based on a smaller sample). The results for the analyses of the molars are more nuanced. The shape index of M₁ in *Paranthropus* is different from *Australopithecus* but not *Ardipithecus* or *Homo*. The shape index of M₂ in *Paranthropus* is not significantly

different from the other genera. For the M_3 , the shape index of *Paranthropus* is significantly different from *Ardipithecus* and *Homo* but not *Australopithecus*. As for the maxillary molars, the shape index of the M^1 of *Homo* is significantly different from *Ardipithecus* and *Australopithecus*, but not *Paranthropus*. For M^2 , *Paranthropus* is only statistically different from *Ardipithecus*. The shape index of the M^3 does not distinguish any of the four genera from each other.

The shape ratios of mandibular premolars in *Homo* are statistically indistinguishable from any of the other genera in our analysis. For the maxillary premolars, both the P^3 and P^4 shape indices are statistically different from *Ardipithecus*, but not *Australopithecus* or *Paranthropus*. The shape index results for mandibular molars of *Homo* vary according to tooth position. The M_1 shape index in *Homo* is only statistically distinct from *Australopithecus*. For M_2 , there are no significant differences between the shape indices of any of the four genera. And for M_3 , *Homo* is only statistically different from *Paranthropus*. Our analyses of the shape indices of the maxillary molars demonstrate that the M^1 of *Homo* is statistically significantly different from *Ardipithecus* and *Australopithecus*, but not *Paranthropus*. The shape index of *Homo* M^2 is only statistically different from that of *Ardipithecus*. None of the four genera can be statistically differentiated by the shape index of their M^3 s.

Mandibular shape indices in *Ardipithecus* are only statistically different from *Paranthropus* for the M_3 ; for all other mandibular teeth (P_4 , M_1 , and M_2), the shape indices of *Ardipithecus* are not statistically different from the other three genera (keeping in mind that we did not include *Ardipithecus* or *Au. anamensis* in the P_3 analysis). In contrast, the maxillary postcanine shape indices of *Ardipithecus* are more distinct: for the P^3 , *Ardipithecus* is significantly different from *Australopithecus* and *Homo*, but not *Paranthropus*. For P^4 , *Ardipithecus* is significantly different from *Homo* but not *Australopithecus* or *Paranthropus*. For M^1 , *Ardipithecus* is only statistically significantly different from *Homo*. For M^2 , *Ardipithecus* is statistically different from *Homo* and *Paranthropus* but not *Australopithecus*, and for the M^3 , *Ardipithecus* is not statistically distinguishable from any of the other genera.

The mandibular shape indices of *Homo* are statistically indistinguishable from the other genera for the P_3 , P_4 , and M_2 . For the M_1 , *Homo* is only different from *Australopithecus*. For the M_3 , *Homo* is only different from *Paranthropus*. As for the maxillary shape indices, *Homo* is distinct from the P^3 , P^4 , M^1 and M^2 of *Ardipithecus* and the M^1 of *Australopithecus*.

FIG. 4. – Box plots of comparative data linear metrics for P_3 . The four panels show box-and-whisker plots for: **A**, mesiodistal (MD) dimension; **B**, buccolingual (BL) dimension; **C**, 2-dimensional area calculated as MDxBL; **D**, shape index calculated as MD/BL. Measurements are in mm.

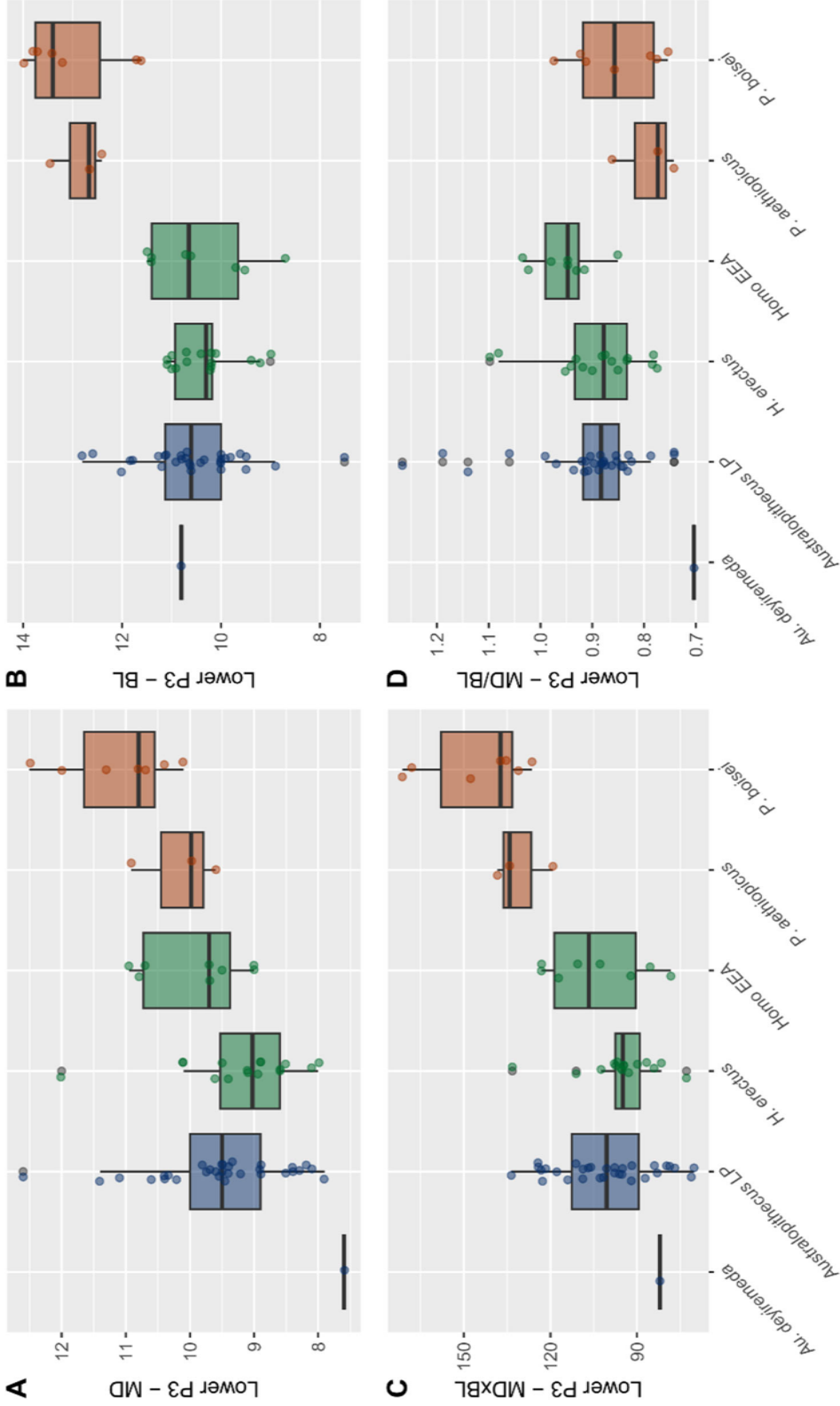


FIG. 5. – Box plots of comparative data linear metrics for P_4 . The four panels show box-and-whisker plots for: **A**, mesiodistal (MD) dimension; **B**, buccolingual (BL) dimension; **C**, 2-dimensional area calculated as MDxBL; **D**, shape index calculated as MD/BL. Measurements are in mm.

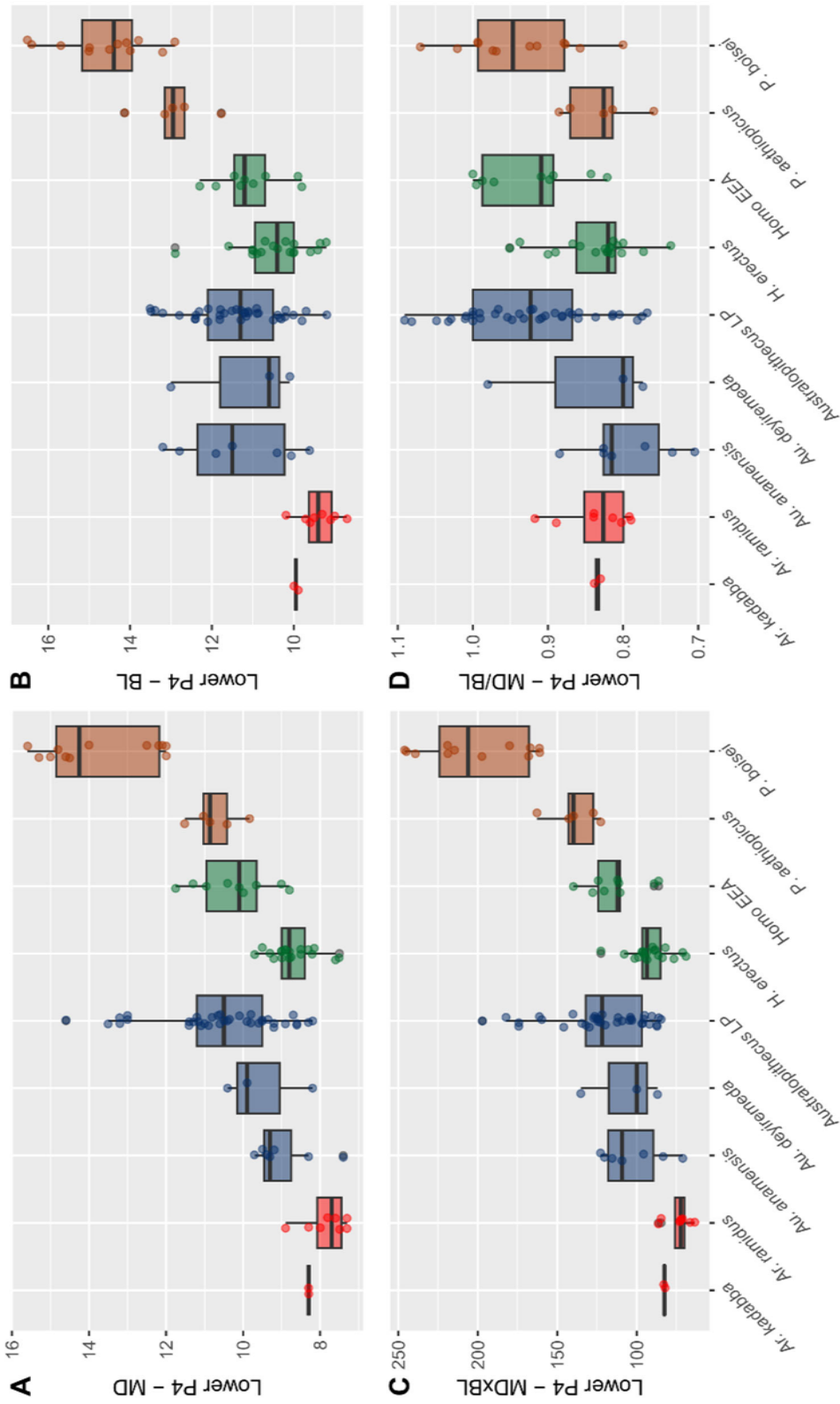


FIG. 6. – Box plots of comparative data linear metrics for M_1 . The four panels show box-and-whisker plots for: **A**, mesiodistal (MD) dimension; **B**, buccolingual (BL) dimension; **C**, 2-dimensional area calculated as MDxBL; **D**, shape index calculated as MD/BL. Measurements are in mm.

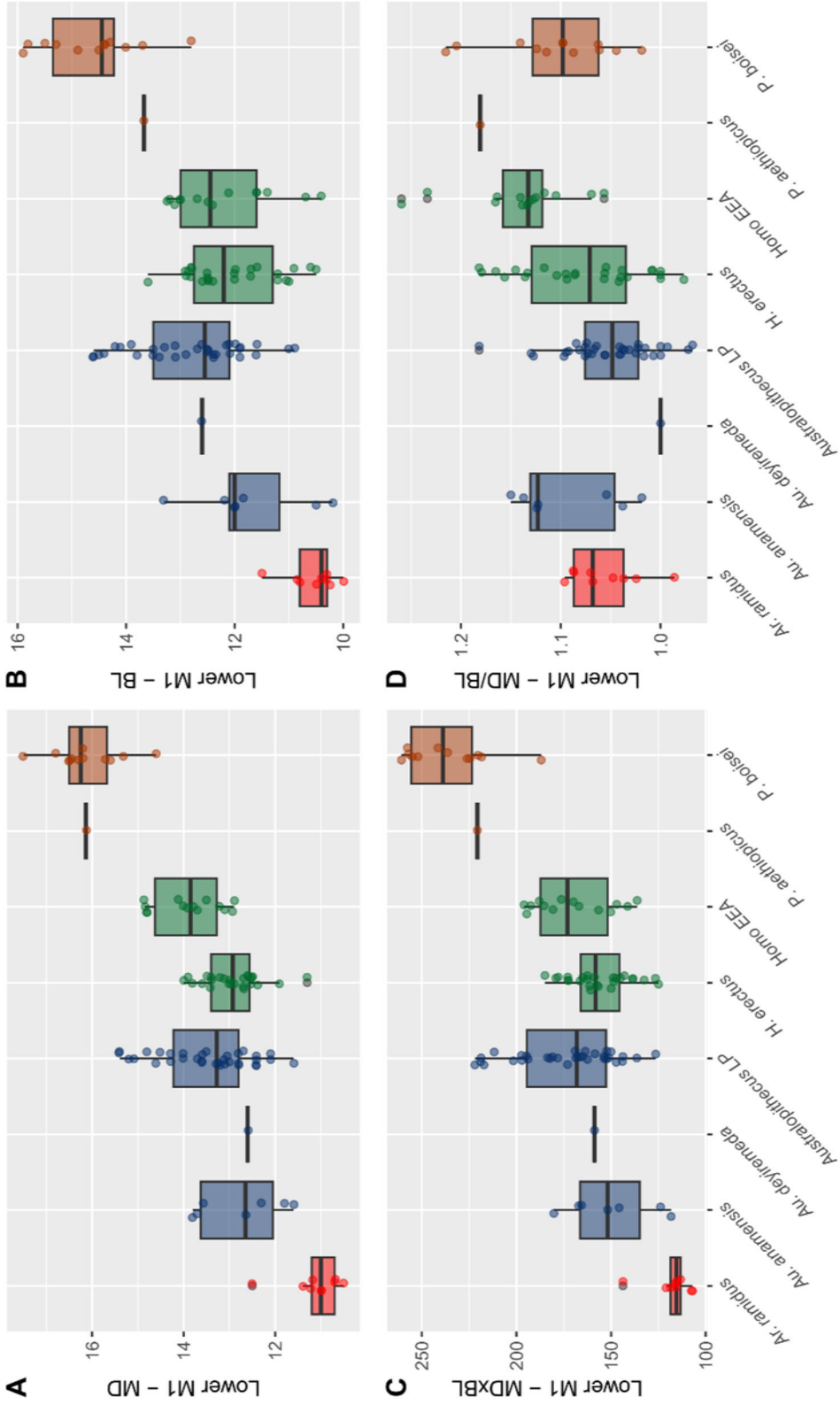


FIG. 7. – Box plots of comparative data linear metrics for M_2 . The four panels show box-and-whisker plots for: **A**, mesiodistal (MD) dimension; **B**, buccolingual (BL) dimension; **C**, 2-dimensional area calculated as MDxBL; **D**, shape index calculated as MD/BL. Measurements are in mm.

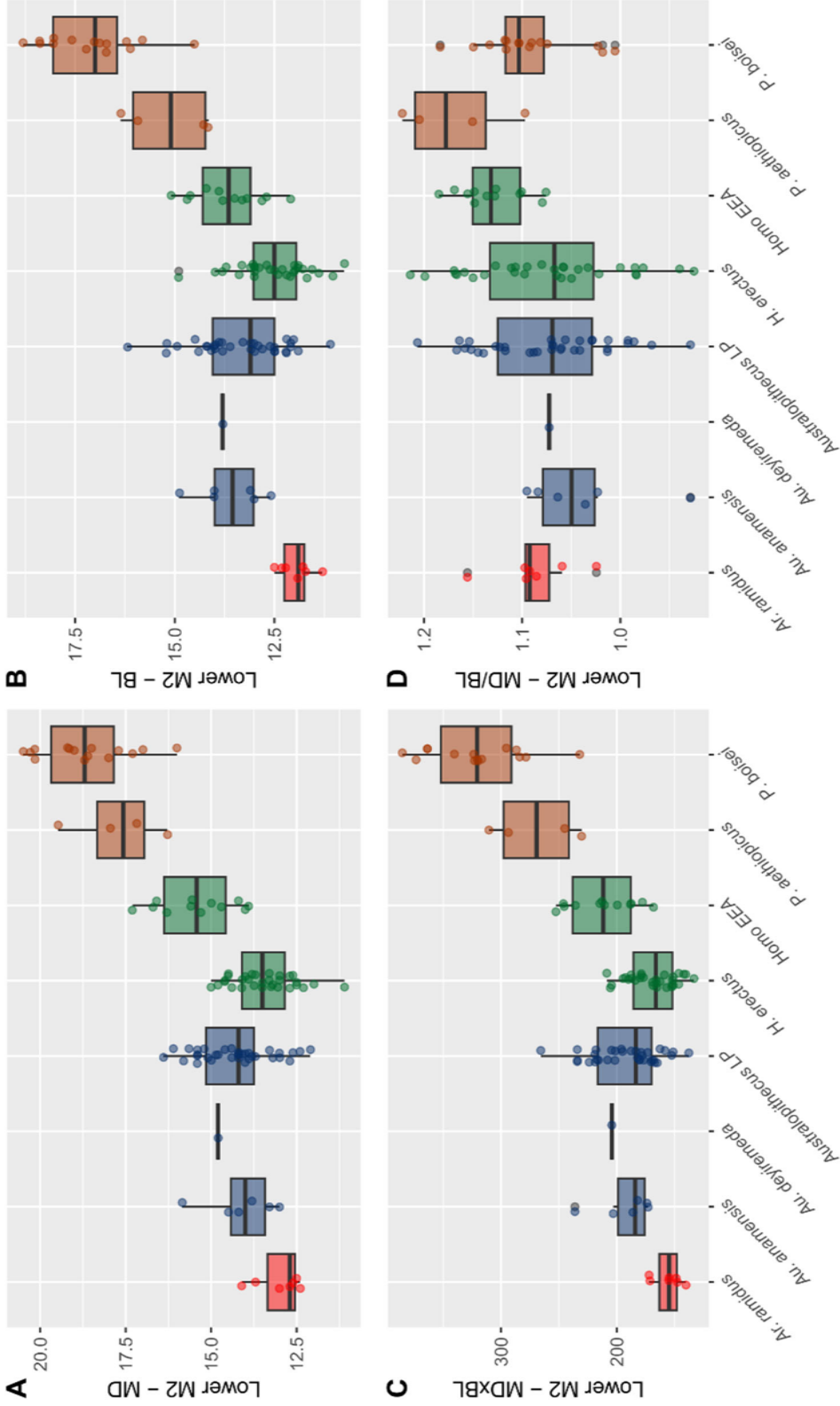
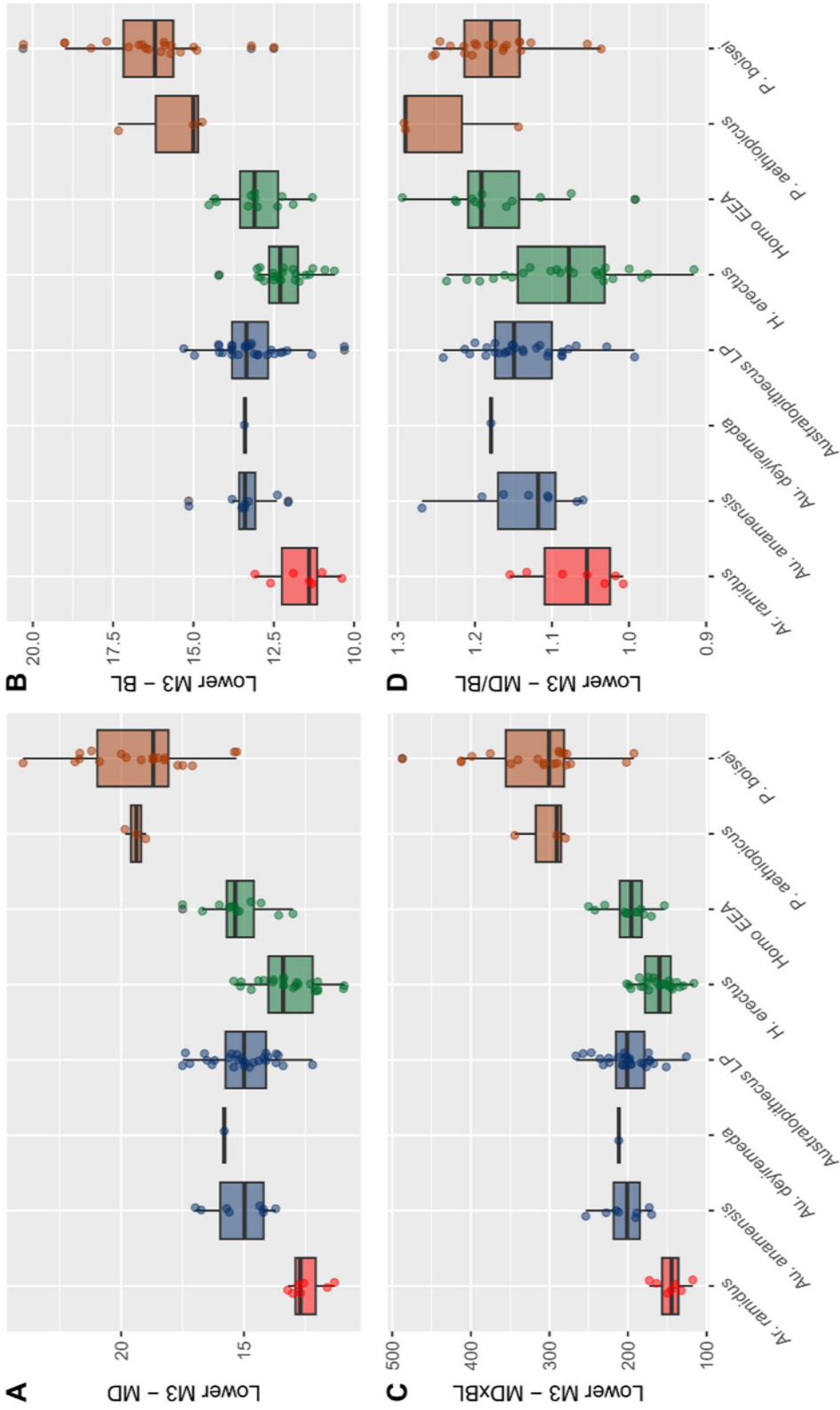


FIG. 8. – Box plots of comparative data linear metrics for M_3 . The four panels show box-and-whisker plots for: **A**, mesiodistal (MD) dimension; **B**, buccolingual (BL) dimension; **C**, 2-dimensional area calculated as MDxBL; **D**, shape index calculated as MD/BL. Measurements are in mm.



210 FIG. 9. – Box plots of comparative data linear metrics for P³. The four panels show box-and-whisker plots for: **A**, mesiodistal (MD) dimension; **B**,
211 buccolingual (BL) dimension; **C**, 2-dimensional area calculated as MDxBL; **D**, shape index calculated as MD/BL. Measurements are in mm.

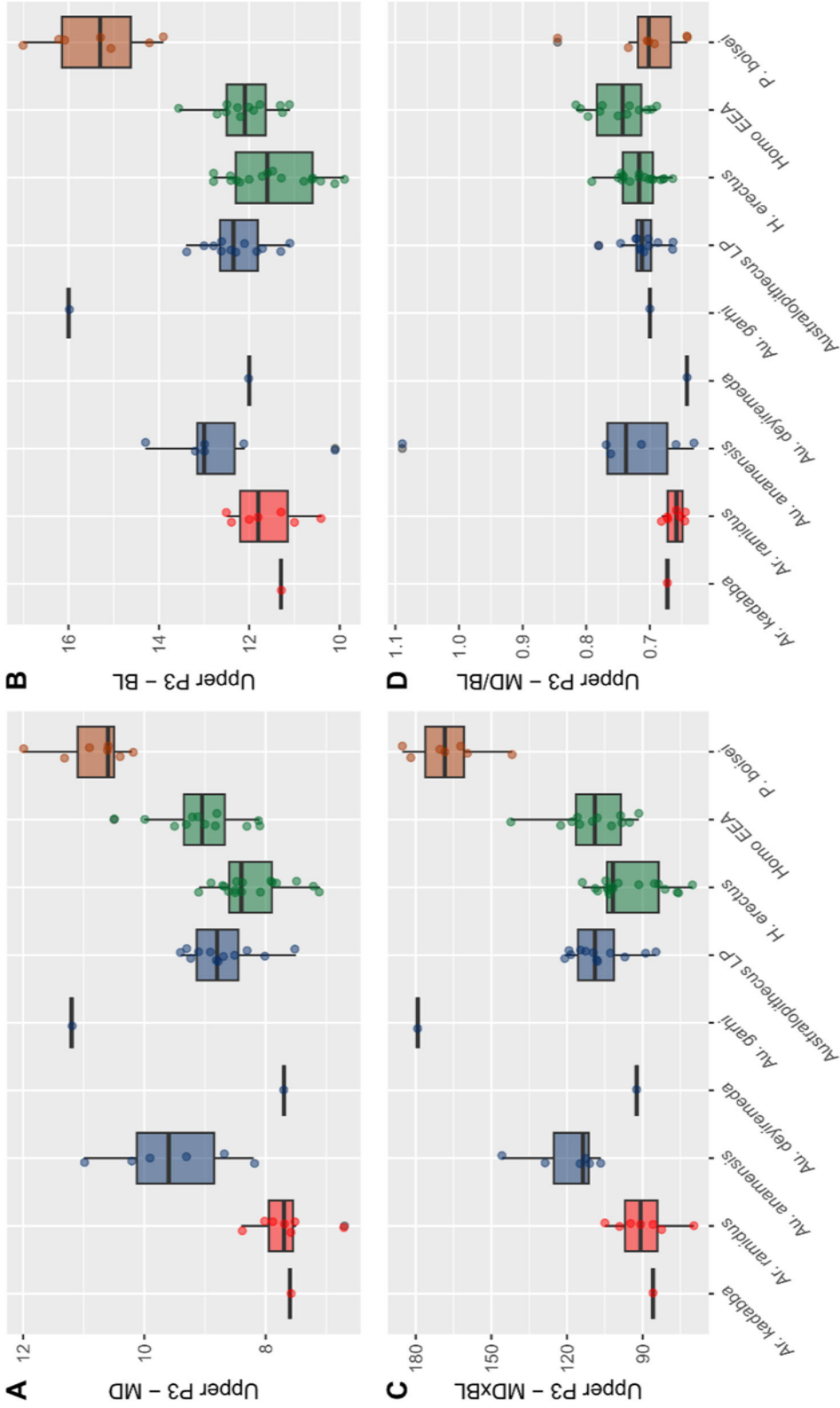


FIG. 10. – Box plots of comparative data linear metrics for P⁴. The four panels show box-and-whisker plots for: **A**, mesiodistal (MD) dimension; **B**, buccolingual (BL) dimension; **C**, 2-dimensional area calculated as MDxBL; **D**, shape index calculated as MD/BL. Measurements are in mm.

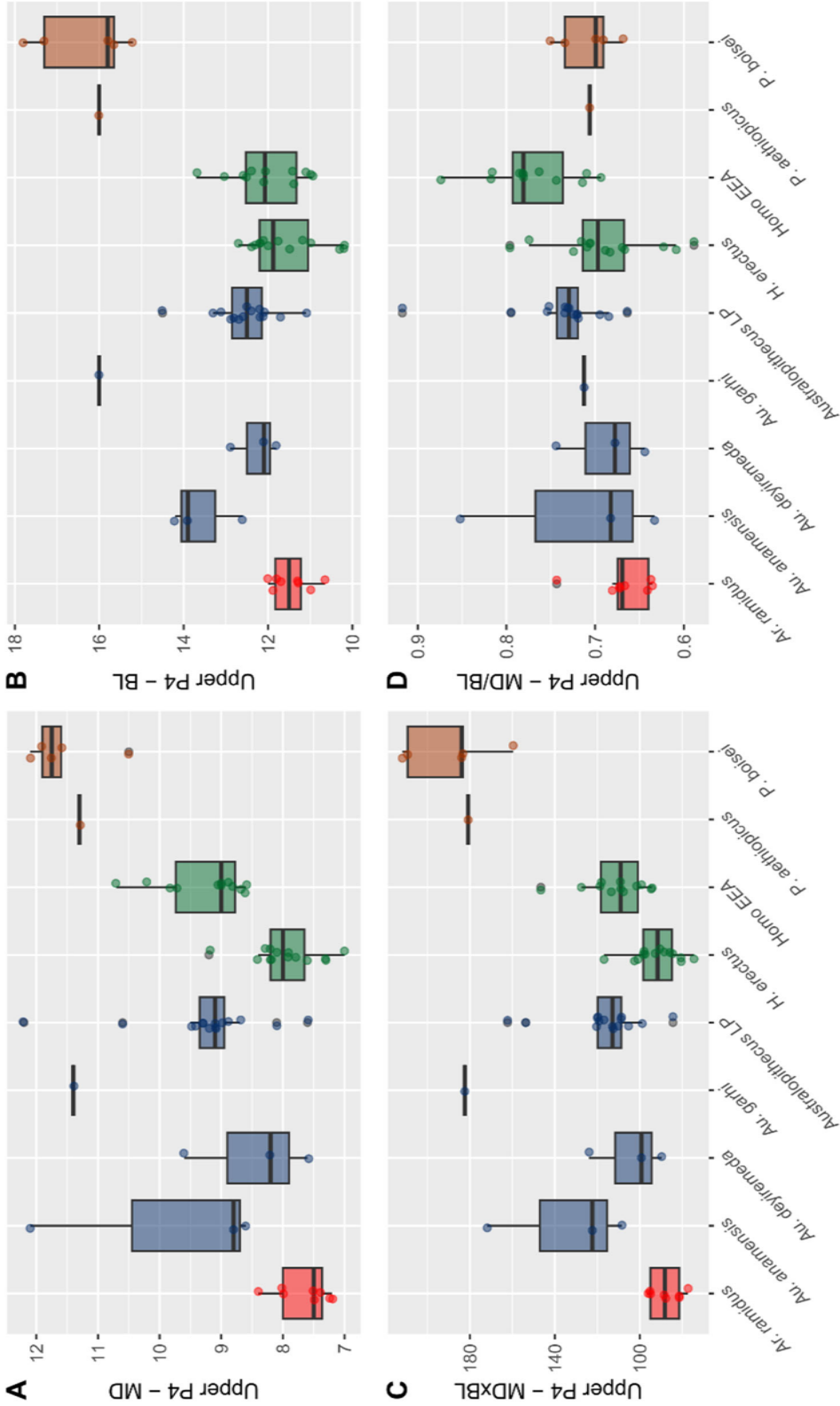


FIG. 11. – Box plots of comparative data linear metrics for M^1 . The four panels show box-and-whisker plots for: **A**, mesiodistal (MD) dimension; **B**, buccolingual (BL) dimension; **C**, 2-dimensional area calculated as MDxBL; **D**, shape index calculated as MD/BL. Measurements are in mm.

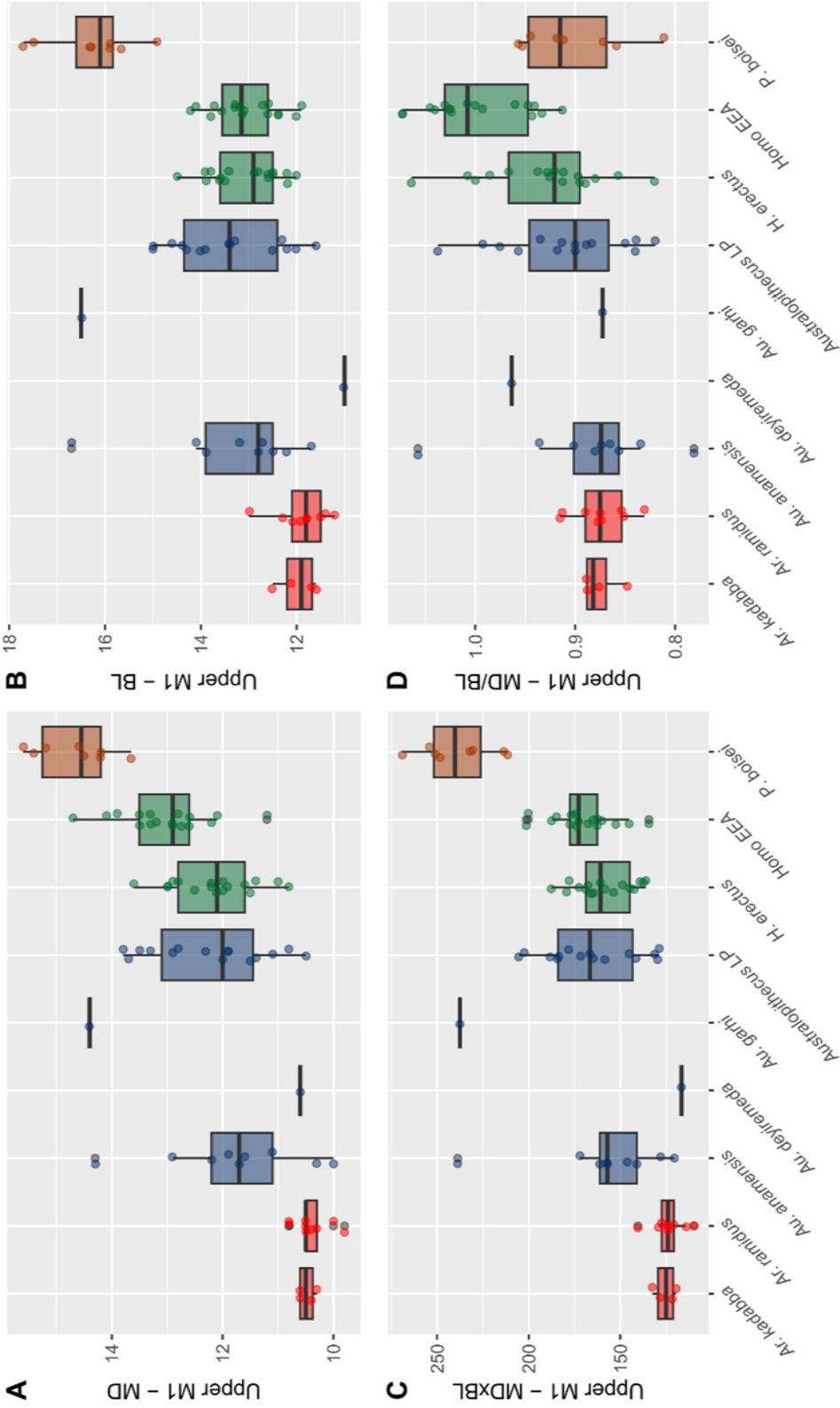


FIG. 12. – Box plots of comparative data linear metrics for M^2 . The four panels show box-and-whisker plots for: **A**, mesiodistal (MD) dimension; **B**, buccolingual (BL) dimension; **C**, 2-dimensional area calculated as MDxBL; **D**, shape index calculated as MD/BL. Measurements are in mm.

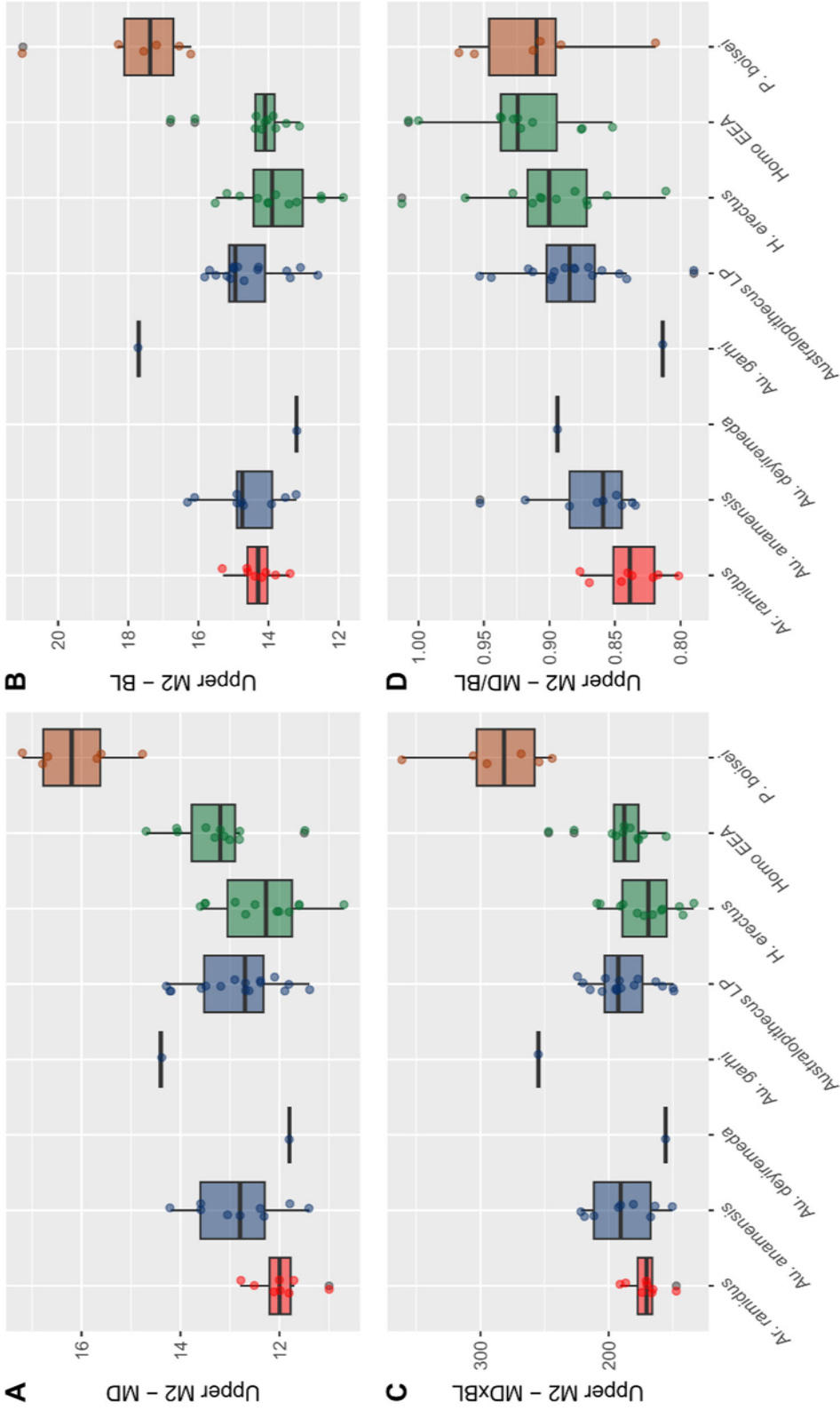
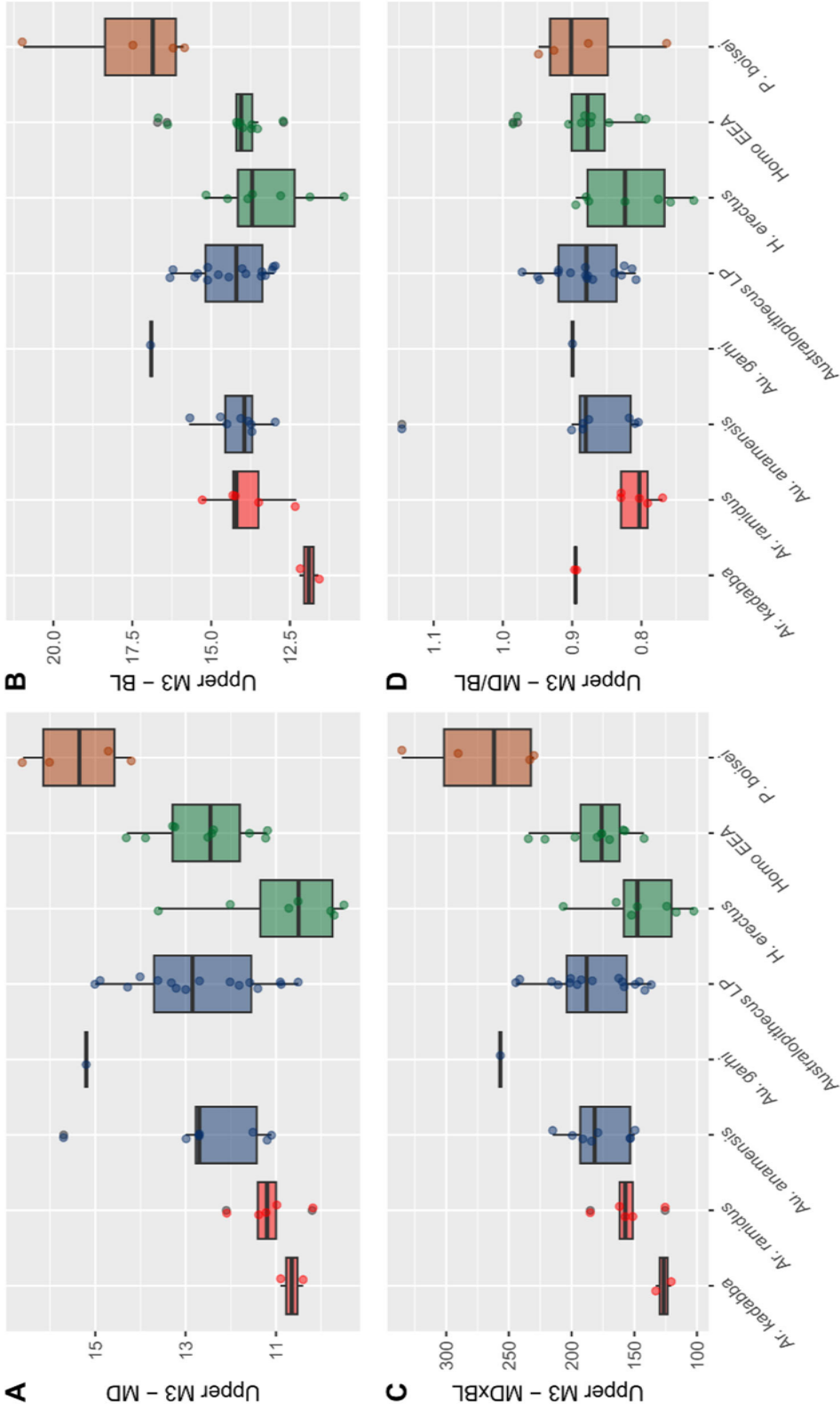


FIG. 13. – Box plots of comparative data linear metrics for M^3 . The four panels show box-and-whisker plots for: **A**, mesiodistal (MD) dimension; **B**, buccolingual (BL) dimension; **C**, 2-dimensional area calculated as MDxBL; **D**, shape index calculated as MD/BL. Measurements are in mm.



Species level analyses: Size measurements (MD, BL, and MDxBL)

This section refers to results presented in Supplemental Tables S6 and S7, and panels A-C of Figs. 4-13. These species-level analyses are statistically more challenging, given that the sample sizes become increasingly smaller as we parcel the sample into tooth type and then into 10 different taxonomic categories.

For the mandibular postcanine dentition, the number of significant differences between species means is low (Supplemental Table S6). In general, we find that linear size metrics of *P. boisei* are statistically different from *Ardipithecus* spp., *Australopithecus* LP, and *H. erectus*, but not statistically distinct from other species of *Australopithecus*, *Homo* EEA, or *P. aethiopicus*. Our data do show that *Ar. ramidus* and *Australopithecus* LP are typically statistically different. And, the MD dimensions of *Homo* EEA and *H. erectus* differentiate them from *Ar. ramidus* and *Australopithecus* LP, and in the case of the M₂, from each other. The BL dimensions do not statistically discriminate well between the non-*Paranthropus* taxa.

The variation within each species' mandibular sample is visually represented in Figs. 4-8. The *Australopithecus* LP sample demonstrates that the larger the sample, the more variation captured, as *Australopithecus* LP variation encompasses almost the full range of variation observed for the MD dimensions of P₃ and P₄ and for the BL dimension of P₃ across all samples, including *Paranthropus* (Figs. 4, 5). However, the average MDxBL size of P₃ and P₄ in *Paranthropus* is larger than the largest specimen of *Australopithecus* LP, indicating that while some mandibular premolars of *Australopithecus* LP are large in either their MD or BL dimension, they are generally not large in both dimensions at the same time, unlike those of *P. boisei*.

The plots of MD and BL molar dimensions show that M₁ best differentiates the smaller size of *Ar. ramidus* from the other taxa, but with considerable overlap in the BL dimension (Figs. 6, 7, 8). The larger size of *Paranthropus* is most noticeable in M₂ and M₃; *Paranthropus* is least different from *Australopithecus* LP in the BL dimension of M₁. There is so much overlap among the taxa assigned to *Australopithecus* and *Homo* that an isolated tooth could only be suggestively assigned to *H. erectus* if it were an M₂ and at the small extreme of the range of variation. There is essentially entire overlap between the molar size dimensions of *Australopithecus* and *Homo* spp. otherwise, especially *Homo* EEA.

Within *Paranthropus*, it is interesting to observe that the BL dimensions of the mandibular premolars are similar between *P. aethiopicus* and *P. boisei*, but the MD dimensions of *P. aethiopicus* falls within the range of variation of *Australopithecus* LP and the other non-robust hominins. For the molars, the pattern is the opposite. The MD dimensions of *P. aethiopicus* and *P. boisei* molars overlap entirely, whereas the BL dimensions of the M₁ and M₂ of *P. aethiopicus* are within the range of *Australopithecus* LP (Figs. 4-8).

The maxillary postcanine dentition comparisons reveal even fewer statistically significant differences than the mandibular analyses (Supplemental Table 7). However, like for the mandibular dentition, *P. boisei* is typically significantly different from the *Ardipithecus* species across all the premolars and molars. *P. boisei* molars are different from the MD dimensions of *Ardipithecus* and *Australopithecus* LP M¹ and M², but not M³. And for all *P. boisei* molars, the linear size measurements are significantly different from *H. erectus*, but not *Homo* EEA.

The box and whisker plots reveal interesting patterns of overlap across the linear size dimensions of the maxillary dentition (Figs. 9-13). The average MD and BL dimensions of P³ increase from *Ar. kadabba* to *Ar. ramidus* to *Australopithecus* LP, with *Au. anamensis* being the largest on average (Figs. 9, 10). *Ar. ramidus* P⁴ MD and BL dimensions are also smaller than *Australopithecus* LP, *Au. anamensis*, and *Au. deyiremeda*, with more overlap in MD dimension with *H. erectus*, and in BL dimension with *Homo* EEA and *H. erectus*.

The BL dimensions of *P. boisei* P³ and P⁴ are more distinct from the other taxa than are the MD dimensions (Figs. 9, 10). This is the same for the sole P⁴ *P. aethiopicus* specimen. While this pattern remains for M¹ and arguably for M³ (the BL dimension of *P. boisei* being more distinct than the MD dimension), for the M² it is the reverse as MD is the more distinct dimension (Figs. 11-13).

For our consideration of isolated maxillary teeth, these box-and-whisker plots reveal a concerning amount of overlap across taxa, especially between *Australopithecus* LP, *Au. anamensis*, *Au. deyiremeda*, *Homo* EEA, and for all but the smallest M³s of *H. erectus* (Figs. 9-13). One complicating factor to our maxillary considerations is *Au. garhi*. We only have one specimen for this taxon, a maxillary dentition. The size of the maxillary postcanine dentition, in all size dimensions, is close to the average of *P. boisei*, above what is observed for other species of *Australopithecus*. Dentally, the feature that associates *Au. garhi* with *Australopithecus* rather than *Paranthropus* is the lack of a reduced anterior dentition (Asfaw *et al.* 1999). Therefore, the size of isolated postcanine teeth of *Au. garhi* will plot within the range of variation observed for *Paranthropus*. Other features will need to be considered in the attempt to differentiate teeth of *Au. garhi* from those of *Paranthropus*.

Species level analyses: Shape (MD/BL)

This section refers to the results presented in Supplemental Tables S6 and S7, and panel D of Figs. 4-13. There are few statistically significant differences in the shape indices of these taxa. P³, P⁴, and M² of *Ar. ramidus* are distinct from *Homo*. *Homo* and *Homo* EEA differ in the shape index of their P⁴, although they vary along a continuum that makes differentiation by individual teeth difficult (Fig. 10). *Homo* EEA is

significantly different from both species of *Ardipithecus*, *Au. anamensis* and *Australopithecus* LP. This is visibly evident in the box-and-whisker plot of Fig. 11, where there is overlap between *Homo* EEA and some of the *Australopithecus* LP specimens, but they mostly segregate. However, to complicate our endeavor, *H. erectus* variation for the M^1 shape index encompasses the full range of variation observed across all our comparative taxa (Fig. 11).

For the mandibular postcanine teeth, the P_4 shape indices of *Au. anamensis* and *Australopithecus* LP are different from each other, as are those of *Australopithecus* LP compared to *H. erectus*, and *Au. anamensis* compared to *P. boisei*. *Australopithecus* LP and *Homo* EEA differ in the shape index of M_1 . And the M_3 shape index of *P. boisei* is statistically different from *Ar. ramidus* and *H. erectus*. Our box-and-whisker plots of the shape ratios (Figs. 4-13) show the considerable overlap between taxa, even for taxa that are statistically significantly different (such as the P_4 of *Australopithecus* LP compared to *Au. anamensis* and *H. erectus*, Fig. 5).

Considering the pattern of overlap observed in the box-and-whisker plots (Figs. 4-13), perhaps the most distinguishable mandibular tooth shape index is that of the M_1 of *Homo* EEA compared to *Australopithecus* LP.

LINEAR DISCRIMINANT (LDA) ANALYSIS

In Table 7 we report the proportion of variance described by LD1 and LD2 for the species and genus level analyses. LD1 presents a proportion of variance placed between 57% and 90% in the species analyses, and between 59.5% to 99.5% in the genus analyses. When LD1 and LD2 are combined, they account for about 88% to 98% of the total variance in the species analyses, and from 95% to 100% in the genus analyses. Therefore, the variance explained is primarily based on the LD1 function. The accuracies of the predictions are between 0.42 to 0.57 in the species analyses, and between 0.47 and 0.69 in the genus analyses. Therefore, these predictions are useful but by no means should they be considered conclusive.

We first discuss the patterns of variance observed in the comparative samples, as this provides the taxonomic framework that we then apply to the Omo teeth. We then present the LDA taxonomic predictions for the Omo teeth.

TABLE 7. – Proportion of variance explained (%) by the discriminant functions and the accuracy of their taxonomic predictions by tooth.

Grouped by	Jaw	Tooth	LD1	LD2	LD1+ LD2	Accuracy of Prediction
Species	Maxilla	P ³	89.44	7.90	97.34	0.48
		P ⁴	80.04	17.06	97.10	0.58
		M ¹	57.70	34.16	91.87	0.49
		M ²	82.59	9.08	91.67	0.48
		M ³	69.21	19.46	88.67	0.42
	Mandible	P ₃	89.81	7.65	97.46	0.48
		P ₄	66.84	24.55	91.40	0.57
		M ₁	56.84	36.32	93.16	0.55
		M ₂	85.14	10.97	96.11	0.52
		M ₃	84.34	12.74	97.07	0.55
Genera	Maxilla	P ³	88.77	7.96	96.73	0.66
		P ⁴	84.80	11.09	95.88	0.66
		M ¹	59.48	37.12	96.60	0.69
		M ²	90.22	8.74	98.96	0.66
		M ³	87.34	12.65	99.99	0.47
	Mandible	P ₃	99.49	0.51	100.00	0.56
		P ₄	79.39	20.25	99.64	0.66
		M ₁	62.39	34.80	97.18	0.68
		M ₂	94.10	5.55	99.64	0.59
		M ₃	90.75	9.22	99.97	0.64

Comparative sample

As shown in the graphical representations from P₃ to M₃ (Figs. 14-18), we see that the common pattern observed for all of these teeth is the differentiation of *Paranthropus* from the other genera (*Ardipithecus*, *Australopithecus* and *Homo*) primarily along LD1. In the bivariate space of LD1 and LD2, there is not much overlap between *Paranthropus* and the other taxa for most teeth, except for P³, and one end of the polygons for P₄-M₃ of *Paranthropus* that overlap with small but dense clusters of *Homo* and *Australopithecus*. For the P³, extensive overlap is observed between *Australopithecus* and *Paranthropus*. Comparison of the species with the genus plots shows that *Au. anamensis* and *Au. garhi* drive this overlap. We see this overlap to some degree for M¹ as well.

P. aethiopicus plots in an intermediate zone between *P. boisei* and *Australopithecus* LP for P₃, P₄, and M₂, and within *P. boisei* for all other teeth for which we have *P. aethiopicus* specimens (P⁴, M₁, and M₃).

Taxa are less clearly differentiated by their placement along LD2. For some teeth, such as P³, P⁴, M¹, and M₁, variation along LD2 differentiates *Ardipithecus* from the other genera. However, for most teeth, *Ardipithecus* has significant overlap with *Homo* and *Australopithecus* in LD1 and LD2 space, and more often with *Homo* than with *Australopithecus*.

For most teeth (all except for P₃), the LD1 versus LD2 plot of the comparative data shows a U-shaped distribution, with *Paranthropus* at one tip and *Ardipithecus* at the other, and with *Australopithecus* and *Homo* taxa distributed in between (Figs. 14-18). From the perspective of wanting to identify isolated teeth, the large region of taxonomic overlap demonstrates that linear metrics and the combined analysis of MD, BL, MDxBL, and MD/BL provides only limited resolution, primarily just for the differentiation of *Paranthropus*, and for some teeth (such as the maxillary and mandibular first molars), *Ardipithecus*.

FIG. 14. – Plots of LD1 and LD2 for P3. Polygons represent the comparative samples. The Omo study specimens are plotted in black and labeled with the specimen number. When specimens are very close to each other, some specimen labels are not shown. This is noted in the text when it occurs. The LD1 and LD2 dimensions for the fossils are reported in Appendix 2. Left panels: species polygons. Right panels: genus polygons. Upper panels: P³. Lower panels: P₃. See keys for symbol codes.

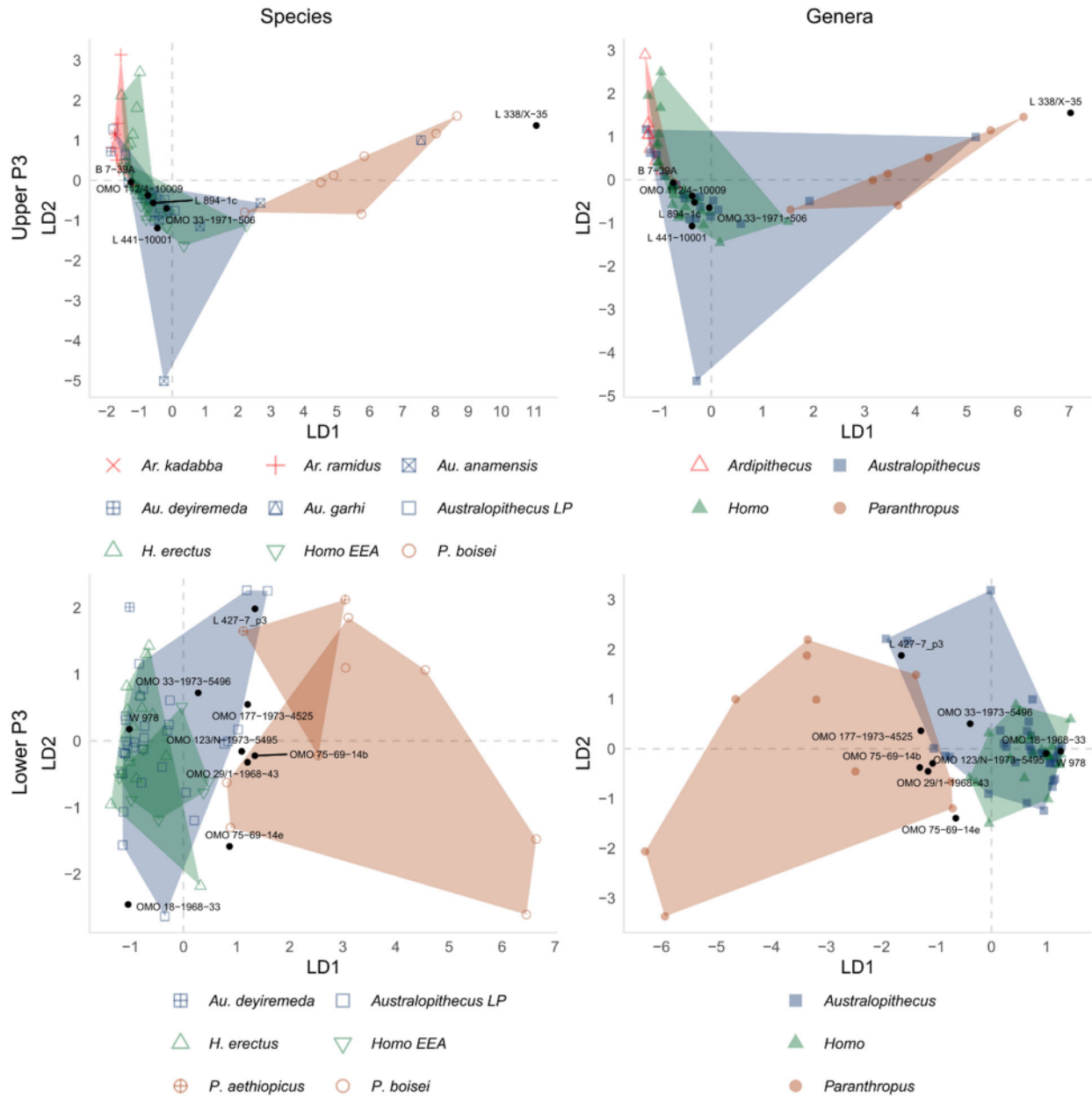


FIG. 15. – LD plots for P4. Polygons represent the comparative samples. The Omo study specimens are plotted in black and labeled with the specimen number. When specimens are very close to each other, some specimen labels are not shown. This is noted in the text when it occurs. The LD1 and LD2 dimensions for the fossils are reported in Appendix 2. Left panels: species polygons. Right panels: genus polygons. Upper panels: P⁴. Lower panels: P₄. See keys for symbol codes.

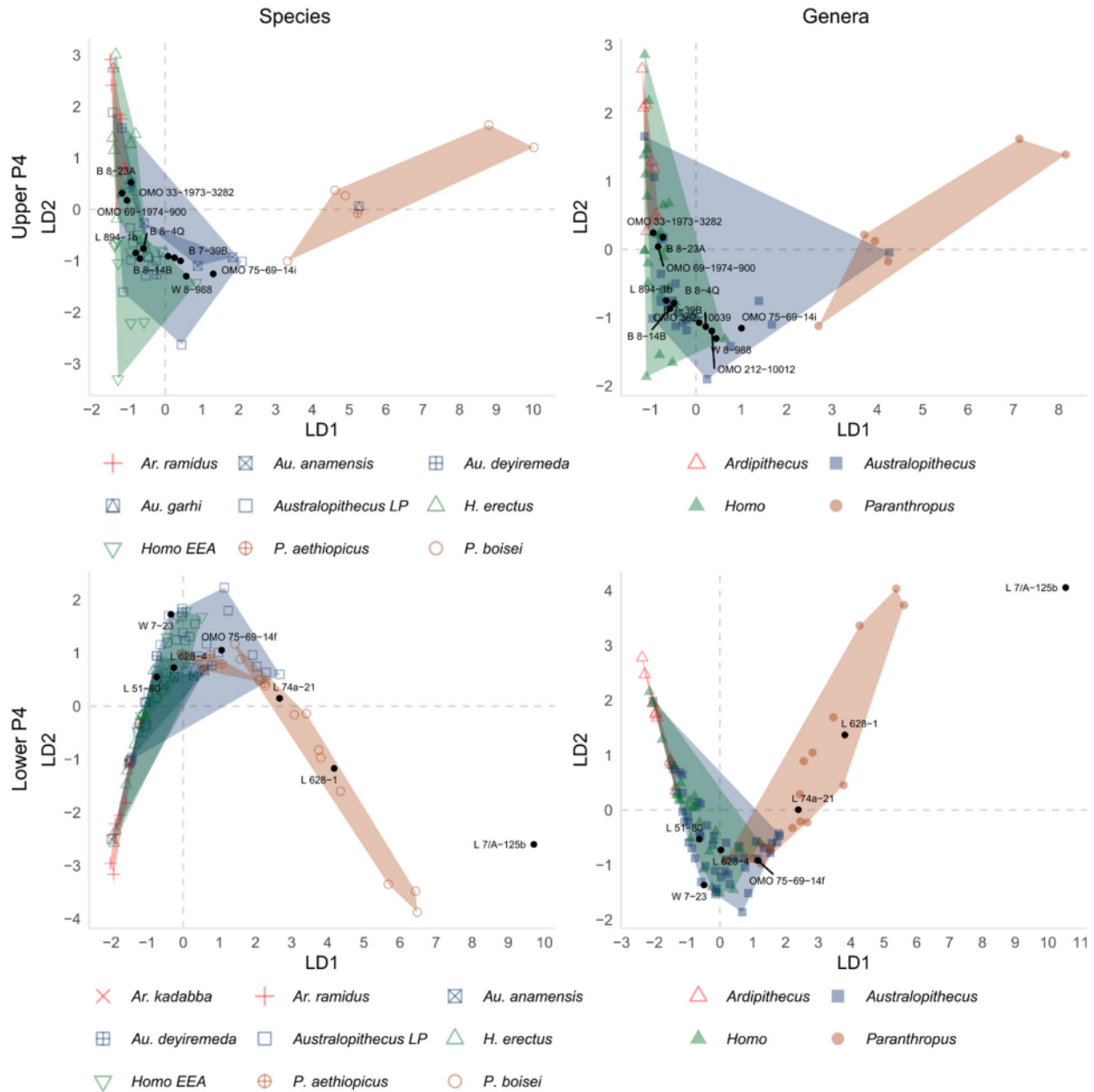


FIG. 16. – LD plots for M1. Polygons represent the comparative samples. The Omo study specimens are plotted in black and labeled with the specimen number. When specimens are very close to each other, some specimen labels are not shown. This is noted in the text when it occurs. The LD1 and LD2 dimensions for the fossils are reported in Appendix 2. Left panels: species polygons. Right panels: genus polygons. Upper panels: M¹. Lower panels: M₁. See keys for symbol codes.

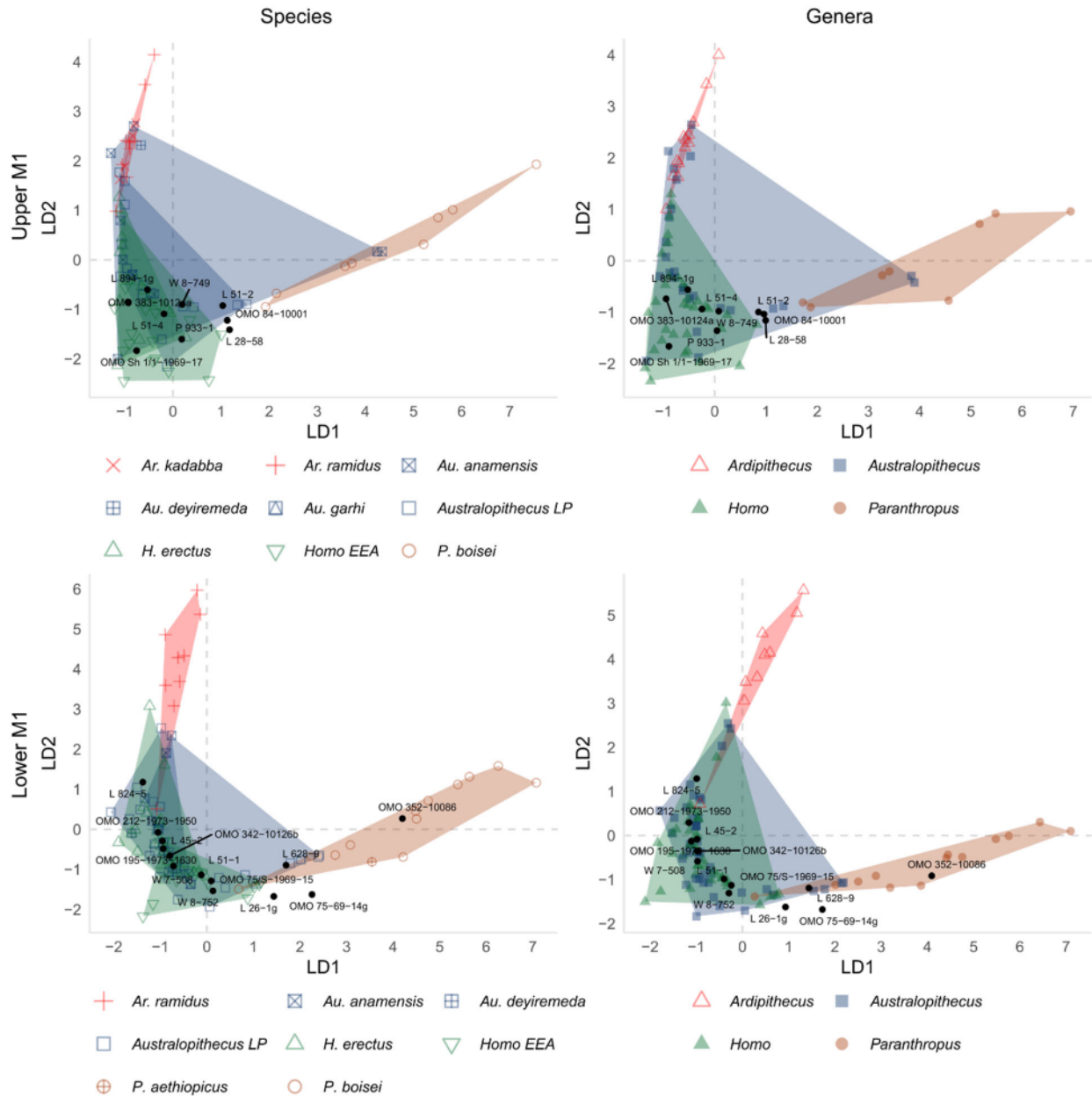


FIG. 17. – LD plots for M2. Polygons represent the comparative samples. The Omo study specimens are plotted in black and labeled with the specimen number. When specimens are very close to each other, some specimen labels are not shown. This is noted in the text when it occurs. The LD1 and LD2 dimensions for the fossils are reported in Appendix 2. Left panels: species polygons. Right panels: genus polygons. Upper panels: M². Lower panels: M₂. See keys for symbol codes.

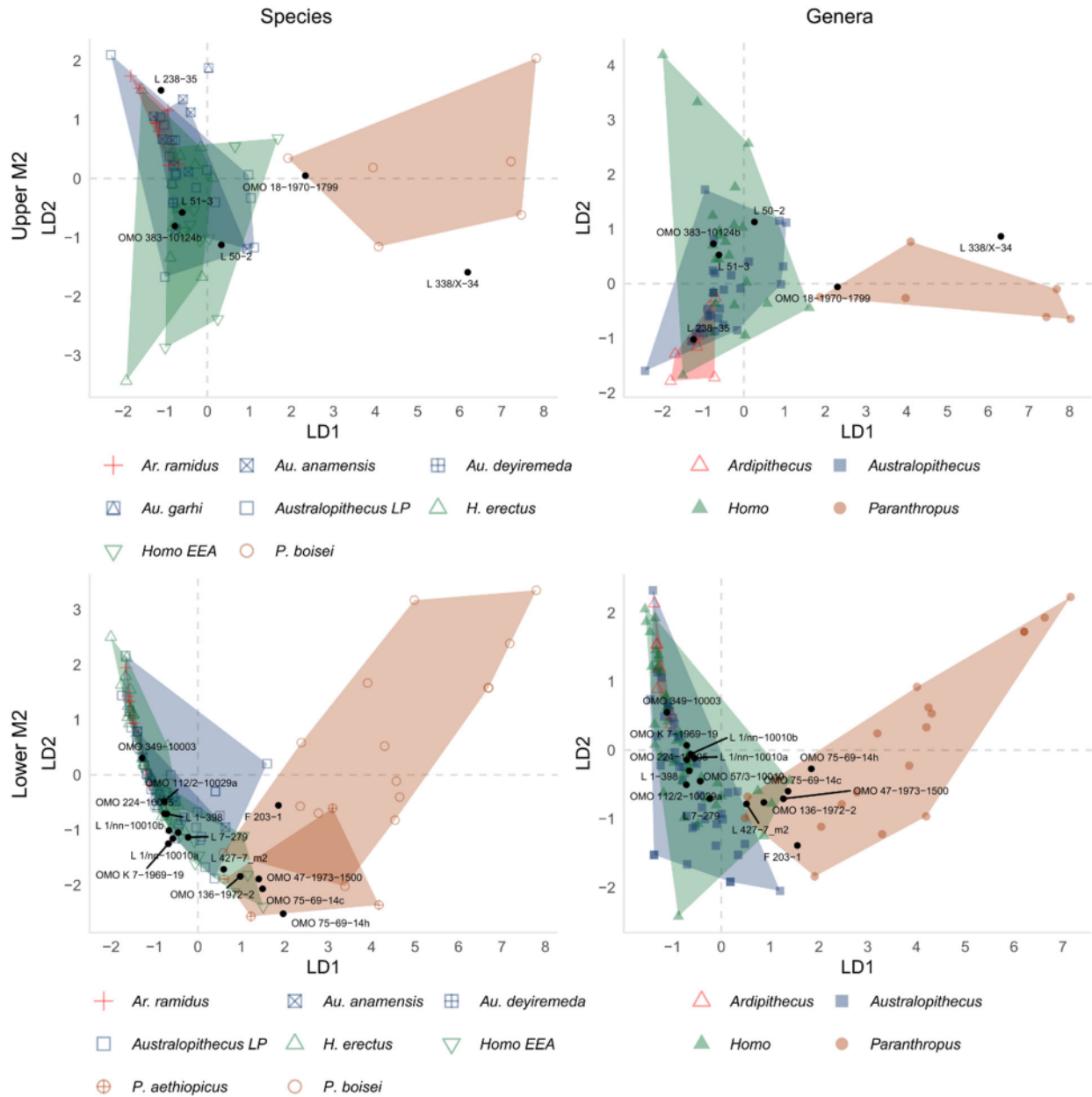
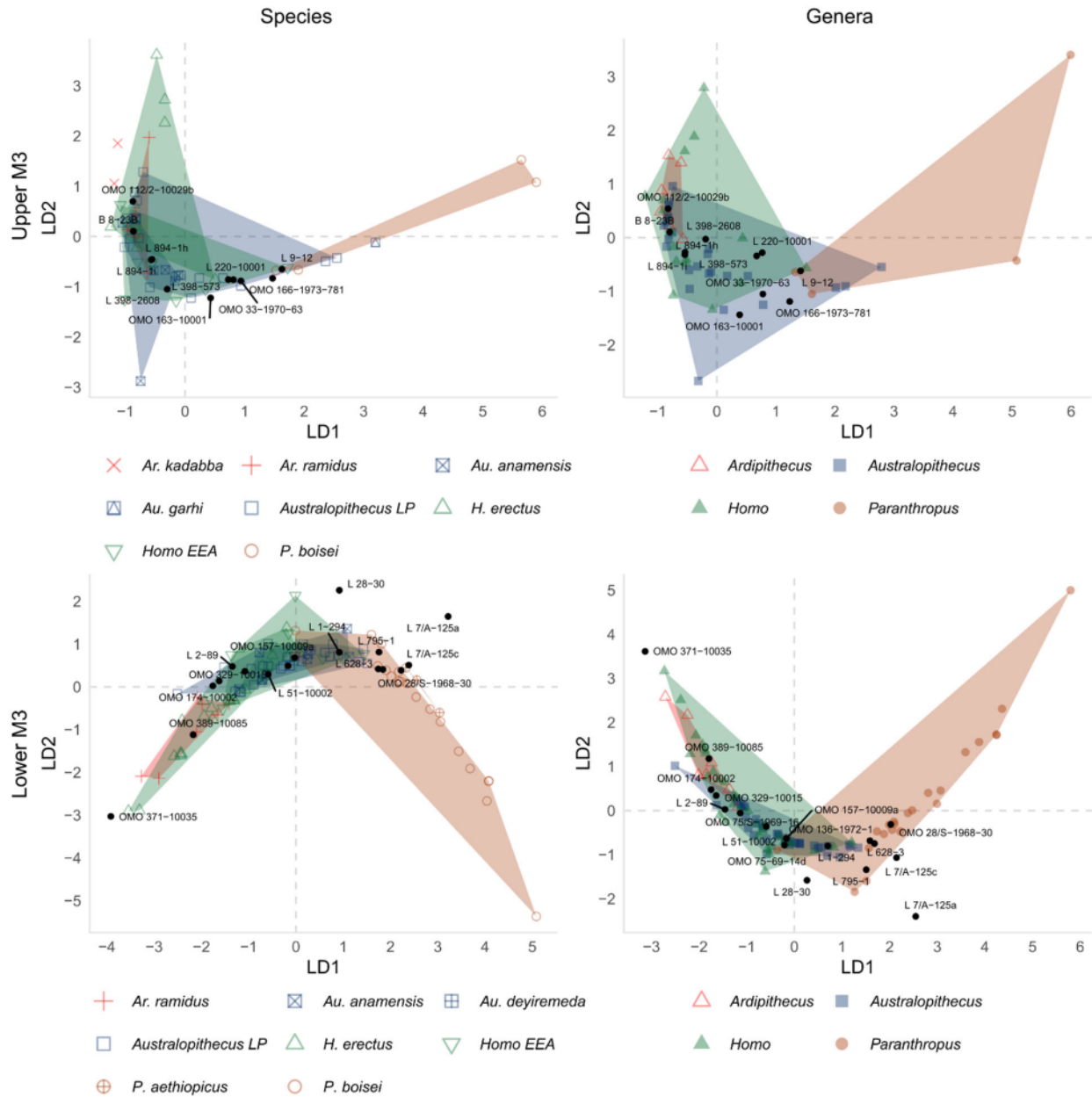


FIG. 18. – LD plots for M3. Polygons represent the comparative samples. The Omo study specimens are plotted in black and labeled with the specimen number. When specimens are very close to each other, some specimen labels are not shown. This is noted in the text when it occurs. The LD1 and LD2 dimensions for the fossils are reported in Appendix 2. Left panels: species polygons. Right panels: Genus polygons. Upper panels: M³. Lower panels: M₃. See keys for symbol codes.



Most-likely taxonomic assignments for the Omo specimens

Table 8 presents the taxonomic predictions for each Omo specimen based on the LDA, which was developed from the comparative dataset. We present the most-likely genus and also the most-likely species. Each specimen is also plotted in Figs. 14-18, showing how it fits within the comparative dataset. The full LDA results are presented in Supplemental Tables S8 for the genus predictions and Supplemental Table S9 for the species predictions.

The likelihood of the prediction provided by LD1 and LD2 ranges from 0.29 to 1.00 (average = 54.7) for species and 0.43 to 1.00 (average = 0.66) for genus. The performance of these LD predictions is represented in the confusion matrices in Supplemental Figs. S2 and S3 for species and genera, respectively. These matrices show a comparison of the original identification for each comparative specimen (the “target”) compared to the prediction for those same comparative data when analyzed using the LDFs. To be clear, the confusion matrix analysis is based only on the comparative dataset, and tests how good our LDF is at predicting the taxon of specimens with known taxonomy (i.e., because they are all in our comparative dataset). In Supplemental Fig. S3, the teeth of the genus *Paranthropus* are predicted as *Paranthropus* in more than 70% of cases for all tooth types with the exception of P₄s and M³s. *Homo* and *Australopithecus* are correctly predicted as their respective genera with less accuracy than *Paranthropus*, and incorrect predictions are frequent between them.

Table 9 summarizes the likelihoods by tooth type for the genus and species estimations. The P₄ has the highest likelihood of correct classification for both genus (0.83) and species (0.76). The M₁, M₃, and P⁴-M³ have the highest likelihoods in the genus LDA. For the species LDA, all teeth save for the P₄ have likelihoods below 0.6, with the maxillary molars having the lowest likelihoods (all three at 0.49 or below). The assignment to genus is not always aligned between the two analyses (one using the comparative data at the genus level, and the second using the comparative data at the species level). The concordance of genus in the by-genus and by-species predictions is presented in the far-right column of Table 9. For both the maxilla and mandible, the P₄ is the most likely to be assigned to the same genus in both analyses. M¹s also tend to be assigned to the same genus in both analyses more often than are the other teeth.

TABLE 8. – LD taxonomic predictions and likelihoods for individual Omo teeth.*

Specimen ID	Mbr	Tooth	Genus Prediction	Likelihood	Species Prediction	Likelihood
B 7-39A	B	P ³	<i>Homo</i> *	43.95	<i>Australopithecus</i> LP	37.21
B 7-39B	B	P ⁴	<i>Australopithecus</i>	74.62	<i>Australopithecus</i> LP	57.69
B 8-4Q	B	P ⁴	<i>Australopithecus</i>	56.43	<i>Australopithecus</i> LP	54.06
B 8-14B	B	P ⁴	<i>Australopithecus</i>	53.63	<i>Australopithecus</i> LP	52.68
B 8-23A	B	P ⁴	<i>Homo</i>	49.74	<i>H. erectus</i>	42.26
B 8-23B	B	M ³	<i>Australopithecus</i>	44.2	<i>Australopithecus</i> LP	33.1
W 7-23	B	P ₄	<i>Australopithecus</i>	78.59	<i>Australopithecus</i> LP	70.09
W 7-508	B	M ₁	<i>Homo</i>	71.32	<i>Homo</i> EEA	35.7
W 8-749	B	M ¹	<i>Australopithecus</i>	66.05	<i>Australopithecus</i> LP	46.32
W 8-752	B	M ₁	<i>Homo</i>	67.9	<i>Homo</i> EEA	43.3
W 8-988	B	P ⁴	<i>Australopithecus</i>	82.25	<i>Australopithecus</i> LP	57.91
W-978	B	P ₃	<i>Australopithecus</i>	54.2	<i>Australopithecus</i> LP	53.5
L 1/nn-10010a	B	M ₂	<i>Homo</i> *	54.9	<i>Australopithecus</i> LP	44.84
L 1/nn-10010b	B	M ₂	<i>Homo</i> *	55.29	<i>Australopithecus</i> LP	46.44
L 1-294	B	M ₃	<i>Australopithecus</i>	73.65	<i>Australopithecus</i> LP	48.47
L 1-398	B	M ₂	<i>Australopithecus</i>	49.14	<i>Australopithecus</i> LP	51.62
L 2-89	B	M ₃	<i>Homo</i> *	63.21	<i>Australopithecus</i> LP	33.15
L 795-1	B	M ₃	<i>Australopithecus</i> *	56.82	<i>P. boisei</i>	48.96
OMO 28/S-1968-30	B	M ₃	<i>Paranthropus</i>	85.43	<i>P. aethiopicus</i>	61.48
OMO 112/2-10029a	B	M ₂	<i>Australopithecus</i>	53.95	<i>Australopithecus</i> LP	53.38
OMO 112/2-10029b	B	M ³	<i>Homo</i> *	43.41	<i>Australopithecus</i> LP	29.22
OMO 112/4-10009	B	P ³	<i>Australopithecus</i>	53.46	<i>Australopithecus</i> LP	43.28
OMO 212-1973-1950	B	M ₁	<i>Homo</i>	80.23	<i>H. erectus</i>	38.9
OMO 212-10012	B	P ⁴	<i>Australopithecus</i>	76.86	<i>Australopithecus</i> LP	56.82
L 45-2	C	M ₁	<i>Australopithecus</i> *	50.1	<i>H. erectus</i>	43
L 51-1	C	M ₁	<i>Homo</i> *	53.63	<i>Australopithecus</i> LP	44.84
L 51-2	C	M ¹	<i>Australopithecus</i>	64.29	<i>Australopithecus</i> LP	48.81
L 51-3	C	M ²	<i>Homo</i> *	50.73	<i>Australopithecus</i> LP	32.12
L 51-4	C	M ¹	<i>Homo</i>	65.42	<i>H. erectus</i>	34.57
L 51-80	C	P ₄	<i>Australopithecus</i>	62.7	<i>Australopithecus</i> LP	55.43
L 51-10002	C	M ₃	<i>Australopithecus</i>	54.35	<i>Australopithecus</i> LP	49.54
L 220-10001	C	M ³	<i>Australopithecus</i>	66.1	<i>Australopithecus</i> LP	47.13
OMO 18-1968-33	C	P ₃	<i>Australopithecus</i>	52.76	<i>Australopithecus</i> LP	49.63
OMO 18-1970-1799	C	M ²	<i>Australopithecus</i>	58.62	<i>Australopithecus</i> LP	42.22
OMO 69-1974-900	C	P ⁴	<i>Homo</i>	56.08	<i>H. erectus</i>	37.04
OMO 84-10001	C	M ¹	<i>Homo</i>	66.42	<i>Homo</i> EEA	43.27
OMO 157-10009a	C	M ₃	<i>Australopithecus</i>	65.49	<i>Australopithecus</i> LP	53.11
OMO 163-10001	C	M ³	<i>Australopithecus</i>	77.89	<i>Australopithecus</i> LP	50.81
OMO 224-10005	C	M ₂	<i>Homo</i> *	51.77	<i>Australopithecus</i> LP	49.78
OMO 329-10015	C	M ₃	<i>Homo</i>	66.31	<i>H. erectus</i>	47.29
OMO 349-10003	C	M ₂	<i>Homo</i>	56.23	<i>H. erectus</i>	50.76

*Highlights specimens for which the genus prediction is discordant between the two analyses.

TABLE 8 (following). – LD taxonomic predictions and likelihoods for individual Omo teeth.*

Specimen ID	Mbr	Tooth	Genus Prediction	Likelihood	Species Prediction	Likelihood
L 9-12	D	M ³	<i>Australopithecus</i>	73.42	<i>Australopithecus</i> LP	61.63
L 50-2	D	M ²	<i>Homo</i>	60.75	<i>Homo</i> EEA	49.07
L 441-10001	D	P ³	<i>Homo</i>	61.3	<i>Homo</i> EEA	48.55
L 824-5	D	M ₁	<i>Australopithecus</i> *	63.77	<i>H. erectus</i>	47.38
L 26-1g	E	M ₁	<i>Homo</i>	65.77	<i>Homo</i> EEA	78.9
L 338/X-34	E	M ²	<i>Paranthropus</i>	100	<i>P. boisei</i>	100
L 338/X-35	E	P ³	<i>Paranthropus</i> *	100	<i>Au. garhi</i>	99.99
OMO 57/3-10010	E	M ₂	<i>Australopithecus</i>	51.23	<i>Australopithecus</i> LP	50.46
OMO 166-1973-781	E	M ³	<i>Australopithecus</i>	79.46	<i>Australopithecus</i> LP	66.17
OMO 177-1973-4525	E	P ₃	<i>Australopithecus</i>	60.6	<i>Australopithecus</i> LP	58.74
L 28-30	F	M ₃	<i>Australopithecus</i> *	80.9	<i>Homo</i> EEA	54.04
L 28-58	F	M ¹	<i>Homo</i>	75.74	<i>Homo</i> EEA	61.27
L 238-35	F	M ²	<i>Australopithecus</i>	71.3	<i>Australopithecus</i> LP	36.22
L 398-573	F	M ³	<i>Australopithecus</i>	66.22	<i>Australopithecus</i> LP	47.42
L 398-2608	F	M ³	<i>Australopithecus</i> *	53.43	<i>Homo</i> EEA	32.35
OMO 33-1970-63	F	M ³	<i>Australopithecus</i>	75.94	<i>Australopithecus</i> LP	60.25
OMO 33-1971-506	F	P ³	<i>Australopithecus</i>	54.47	<i>Australopithecus</i> LP	37.35
OMO 33-1973-3282	F	P ⁴	<i>Homo</i>	61.2	<i>H. erectus</i>	43.84
OMO 33-1973-5496	F	P ₃	<i>Australopithecus</i>	65.23	<i>Australopithecus</i> LP	64.28
OMO 123/N-1973-5495	F	P ₃	<i>Australopithecus</i>	61.28	<i>Australopithecus</i> LP	61.71
OMO 174-10002	F	M ₃	<i>Homo</i>	66.77	<i>H. erectus</i>	51.8
OMO 371-10035	F	M ₃	<i>Ardipithecus</i>	94.06	<i>Ar. ramidus</i>	85.89
P 933-1	F	M ¹	<i>Homo</i>	81.66	<i>Homo</i> EEA	59.97
L 7-279	G	M ₂	<i>Australopithecus</i>	56.36	<i>Australopithecus</i> LP	51.01
L 7/A-125a	G	M ₃	<i>Paranthropus</i>	82.99	<i>P. boisei</i>	97.76
L 7/A-125b	G	P ₄	<i>Paranthropus</i>	100	<i>P. boisei</i>	100
L 7/A-125c	G	M ₃	<i>Paranthropus</i>	82.03	<i>P. boisei</i>	88.78
L 74/A-21	G	P ₄	<i>Paranthropus</i>	86.94	<i>P. boisei</i>	76.86
L 427-7_m2	G	M ₂	<i>Australopithecus</i> *	57.96	<i>Homo</i> EEA	56.99
L 427-7_p3	G	P ₃	<i>Australopithecus</i> *	51	<i>P. aethiopicus</i>	65.19
L 628-1	G	P ₄	<i>Paranthropus</i>	99.93	<i>P. boisei</i>	99.94
L 628-3	G	M ₃	<i>Paranthropus</i>	61.35	<i>P. boisei</i>	58.64
L 628-4	G	P ₄	<i>Australopithecus</i>	72.88	<i>Australopithecus</i> LP	55.64
L 628-9	G	M ₁	<i>Australopithecus</i>	66.72	<i>Australopithecus</i> LP	68.75
L 894-1b	G	P ⁴	<i>Australopithecus</i>	48.9	<i>Australopithecus</i> LP	50.1
L 894-1c	G	P ³	<i>Australopithecus</i>	48	<i>Australopithecus</i> LP	38.1
L 894-1g	G	M ¹	<i>Australopithecus</i>	57.9	<i>Australopithecus</i> LP	40.7
L 894-1h	G	M ³	<i>Australopithecus</i>	53.7	<i>Australopithecus</i> LP	37.1
L 894-1i	G	M ³	<i>Australopithecus</i>	54.4	<i>Australopithecus</i> LP	37.4
OMO Sh 1/1-1969-17	G	M ¹	<i>Homo</i>	89.71	<i>Homo</i> EEA	73.5
OMO 29/1-1968-43	G	P ₃	<i>Australopithecus</i>	59.53	<i>Australopithecus</i> LP	60.4

*Highlights specimens for which the genus prediction is discordant between the two analyses.

TABLE 8 (following). – LD taxonomic predictions and likelihoods for individual Omo teeth.*

Specimen ID	Mbr	Tooth	Genus Prediction	Likelihood	Species Prediction	Likelihood
OMO 47-1973-1500	G	M ₂	<i>Australopithecus</i> *	54.46	<i>Homo</i> EEA	50.66
OMO 75/S-1969-15	G	M ₁	<i>Homo</i> *	58.24	<i>Australopithecus</i> LP	36.98
OMO 75/S-1969-16	G	M ₃	<i>Homo</i> *	57.98	<i>Australopithecus</i> LP	38.53
OMO 75-1969-14b	G	P ₃	<i>Australopithecus</i>	56.85	<i>Australopithecus</i> LP	58.52
OMO 75-1969-14c	G	M ₂	<i>Australopithecus</i> *	50.23	<i>P. aethiopicus</i>	47.81
OMO 75-1969-14d	G	M ₃	<i>Australopithecus</i>	68.38	<i>Australopithecus</i> LP	57.15
OMO 75-1969-14e	G	P ₃	<i>Australopithecus</i>	56.72	<i>Australopithecus</i> LP	54.5
OMO 75-1969-14f	G	P ₄	<i>Australopithecus</i>	81.17	<i>Australopithecus</i> LP	71.5
OMO 75-1969-14g	G	M ₁	<i>Homo</i> *	51.39	<i>P. aethiopicus</i>	52.59
OMO 75-1969-14h	G	M ₂	<i>Paranthropus</i>	53	<i>P. aethiopicus</i>	87.33
OMO 75-1969-14i	G	P ⁴	<i>Australopithecus</i>	90.7	<i>Au. anamensis</i>	45.8
OMO 136-1972-1	G	M ₃	<i>Paranthropus</i>	56.02	<i>P. boisei</i>	49.39
OMO 136-1972-2	G	M ₂	<i>Australopithecus</i> *	57.8	<i>Homo</i> EEA	60.53
OMO 195-1973-1630	G	M ₁	<i>Homo</i>	75.26	<i>H. erectus</i>	39.58
OMO 352-10086	J	M ₁	<i>Paranthropus</i>	99.99	<i>P. boisei</i>	99.99
F 203-1	K	M ₂	<i>Australopithecus</i>	59.92	<i>Australopithecus</i> LP	44.24
OMO 362-10039	K	P ⁴	<i>Australopithecus</i>	72.19	<i>Australopithecus</i> LP	58.42
OMO 342-10126b	L	M ₁	<i>Homo</i>	67.91	<i>H. erectus</i>	39.71
OMO 383-10124a	L	M ¹	<i>Homo</i>	74.66	<i>H. erectus</i>	36.68
OMO 383-10124b	L	M ²	<i>Homo</i>	58.27	<i>H. erectus</i>	36.54
OMO 389-10085	L	M ₃	<i>Homo</i>	60.31	<i>H. erectus</i>	66.81
OMO K 7-1969-19	L	M ₂	<i>Homo</i>	61.25	<i>Homo</i> EEA	40.44

*Highlights specimens for which the genus prediction is discordant between the two analyses.

TABLE 9. – Summary of LDA likelihoods for the Omo taxonomic predictions by tooth type.

	n	Avg likelihood for genus prediction	Avg likelihood for species prediction	Number of times the genus is a mismatch
P ³	6	60.20	50.75	2 (33%)
P ⁴	11	65.69	50.60	0
M ¹	9	69.89	49.44	0
M ²	6	66.61	49.36	1 (17%)
M ³	10	62.56	45.69	2 (20%)
P ₃	9	57.57	58.50	1 (11%)
P ₄	7	83.17	75.64	0
M ₁	13	67.61	52.06	4 (31%)
M ₂	15	54.90	52.42	7 (47%)
M ₃	17	69.18	58.28	4 (24%)

MORPHOLOGICAL SCORES

Figs. 19 and 20 show the four dendrograms from the hierarchical clustering analysis of the morphological traits scored for the Omo premolars and molars, respectively. The analyses return three as the optimal number of clusters in all of the dendrograms except for the lower molars, which is best categorized into four major clusters. At the bottom of each dendrogram in Figs. 19 and 20, we include two rows of taxonomic symbols reporting the taxon predicted from our LDA (Table 8). The genus prediction is reported in the upper row and the species prediction in the lower row. For specimens with only one symbol, the genus prediction matches between the two analyses.

In the upper premolars dendrogram (Fig. 19), there are 14 specimens categorized into three main clusters. The LDA (Table 8) categorized five of these specimens to *Homo*, eight to *Australopithecus*, and one to *Paranthropus/Au. garhi*. These taxa are distributed across the three clusters, although one of the three main clusters has four *Homo* specimens and three *Australopithecus*. Two elements of the same specimen (L 894-1b and L-894-1c) that are attributed to *Australopithecus* by our LDA, but to *H. habilis* by Boaz & Howell (1977), are within this same main cluster but in separate sub-clusters. It is also interesting to note that these two individuals – found in Member G – show the highest similarities in the dendrogram with two other specimens attributed to *Homo* in the LDA, one from Usno Formation (B 8-23A, equivalent to lower Member B) and other from Member F (OMO 33-1973-3282). Because the morphological scoring system we employed was originally designed to characterize dental variation in *Homo sapiens*, it is possible that this approach is better at clustering *Homo* compared to other hominin taxa, though it is not perfect.

The lower premolars dendrogram (Fig. 19) is also divided into three main clusters. Among the 18 specimens, the LDA (Table 8) classified 10 of them to *Australopithecus*, and the remaining eight to *Paranthropus*. It is noteworthy that among the most similar specimens, there is a pair of P₃s and a pair of P₄s that each include both a *P. aethiopicus* and an *Australopithecus* specimen. For the P₃s, one corresponds to *P. aethiopicus* (L 398-120; Table 3), while the other (L 427-7) is attributed to *Australopithecus* (51%) in the genus predictions but *P. aethiopicus* in the species predictions (65%, Table 8). Morphologically, both specimens exhibit the same grades for the analyzed traits and are similar in their BL diameters, whereas for the MD diameters L 398-120 is larger. Concerning the P₄s, one corresponds to *P. aethiopicus* (L 51-79; Table 3), while the other (L 51-80) is attributed to *Australopithecus* (63%) and *Au. LP* (55%, Table 8). Morphologically, both specimens show the same grades for the analyzed traits, however, they do differ in their MD and BL diameters, with L 51-79 being larger than L 51-80.

The upper molars dendrogram (Fig. 20) is also categorized into three main clusters. There are 23 specimens that the LDA categorized as follows: eight *Homo*, 14 *Australopithecus*, and one *Paranthropus*. The most similar specimens in this plot are two *Homo*: the M¹ P 933-1 assigned to *Homo* EEA (60%) and the M² OMO 383-10124b assigned to *H. erectus* (37%) (Table 8).

The lower molars are the most abundant, with 39 specimens clustered in four main groups (Fig. 20). The LDA categorize 13 *Homo*, 15 *Australopithecus*, 10 *Paranthropus*, and one *Ardipithecus* (Table 8). In this group, there are two sets of likely M₂ antimeres that cluster together: L 1/nn-10010a and L 1/nn-10010b, and OMO 75-1969-14c and OMO 75-1969-14h. The teeth in the first set are attributed to *Homo* (55%) and *Australopithecus LP* (45%). Within the second set, OMO 75-1969-14c is assigned to *Australopithecus* (50%) and *P. aethiopicus* (48%), and OMO 75-1969-14 is assigned to *Paranthropus* (53%) and *P. aethiopicus* (87%) (Table 8).

In summary, the results of our dendrograms show that for the Omo sample, there is no clear morphological scoring pattern for each genus and/or species that can be used to establish consistent differences between them. These results indicate that morphological scores alone, as currently formally established, do not adequately distinguish between the hominin taxa present in the Omo.

FIG. 19. – Dendrograms from the hierarchical analysis of Omo morphological trait scores for upper and lower premolars. The symbols between the specimen labels and the tips of the dendrogram represent the genus predictions from our LD analyses (Table 8). The specimens that have a second symbol below the top row were predicted to have a different genus in the species-level LDA prediction. This second genus is reflected by the shape and color of the second symbol. These results are discussed in detail in section Morphological Scores. Although the cluster analysis returned three as the most appropriate number of categories, these three clusters do not reflect genera. Notes also the frequency with which specimens assigned to different genera are the closest pair to each other.

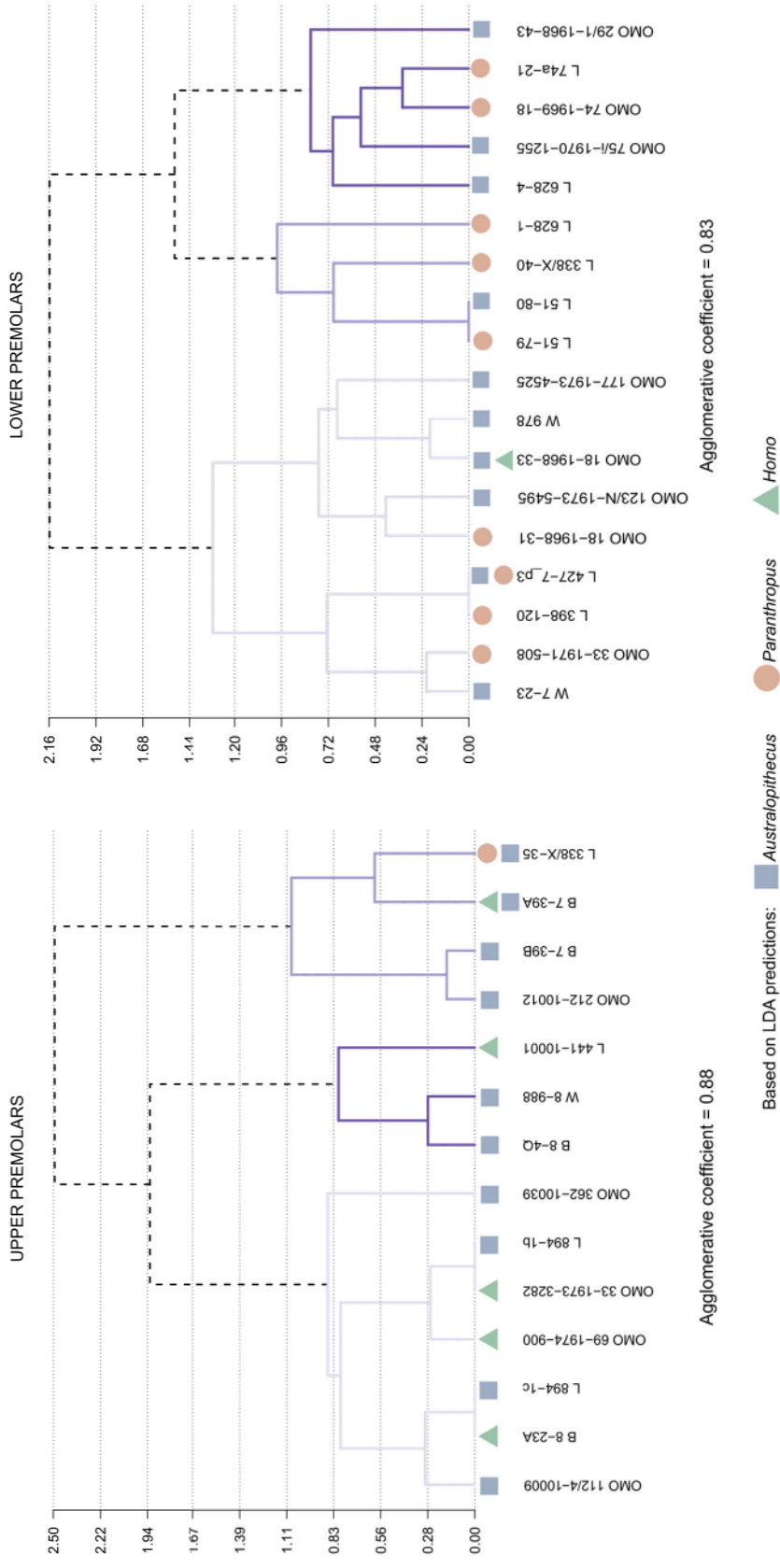
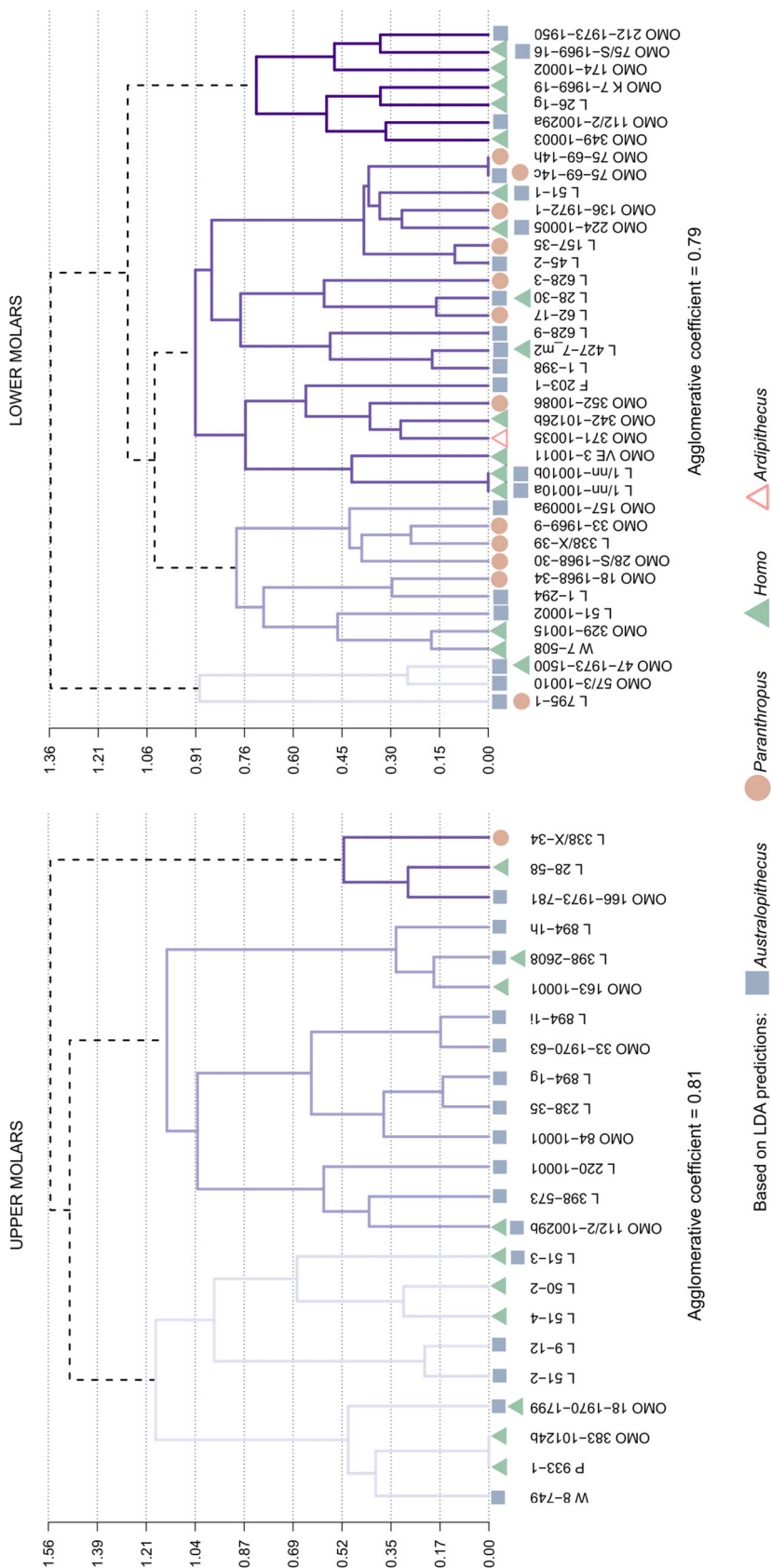


Fig. 20. – Dendrograms from the hierarchical analysis of Omo morphological trait scores for upper and lower molars. The symbols between the specimen labels and the tips of the dendrogram represent the genus predictions from our LD analyses (Table 8). The specimens that have a second symbol below the top row were predicted to have a different genus in the species-level LDA prediction. This second genus is reflected by the shape and color of the second symbol. These results are discussed in detail in section Morphological Scores. The maxillary molars are clustered into three groups, but Homo and Paranthropus are intermixed in all of them. The lower molars are clustered into four groups, but again the main clusters are combinations of genera rather than discriminatory.



MOLAR CUSP AREAS

In Figs. 21 and 22, we present the results of the hierarchical clustering analyses of the molar and premolar cusp areas combined with the taxonomic assignments from the LDA. This approach enables us to explore the relationship between variation in cusp area and linear size dimensions.

The distinction between specimens assigned to *Paranthropus* and those assigned to other groups is evident for the lower molars when comparing cusp proportions and cusp size (Fig. 21). When the lower molars are grouped into an optimal number of clusters using the silhouette method, there are two groups identified when all cusps are compared. One of these groups contains no specimens assigned to *Paranthropus* at either the genus or species level, based on the LDA results. Out of the 15 teeth in the *Paranthropus* cluster, five do not have *Paranthropus* predicted as either the genus or species based on the LDA results (all have a genus classification of *Australopithecus*: L1-294, OMO 157-1000a, OMO 47-1973-1500, L 628-9, L 28-30). This distinction is even clearer when only the four main cusps are compared, with the *Paranthropus* cluster containing only two specimens not assigned to *Paranthropus* at either the genus or species level (L 1-294 and OMO 47-1973-1500), and the non-*Paranthropus* cluster containing only one tooth LDA-assigned to *Paranthropus* (OMO 18-1968-34). This applies to all three lower molars combined and is driven primarily by the increased absolute size of the cusps in *Paranthropus*. This result suggests that tooth size alone is a reliable trait for differentiating between *Paranthropus* and non-*Paranthropus* specimens, with the exception that the group *Paranthropus* may contain a small number of *Australopithecus* teeth (based on the LDA results). There is also evidence that cusp area proportions are useful in distinguishing between *Homo* and *Australopithecus*, with six of the *Homo* teeth (based on LDA results) forming a cluster when all cusps are considered. When only the four main cusps are considered, there appears to be no distinction between *Australopithecus* and *Homo*.

For upper molars, the differences among the species/genera are less defined, and much smaller samples were available for comparisons (e.g., one tooth for *Paranthropus*; Fig. 22). Groupings tend to cluster more by tooth type than taxon, although due to sample size limitations, further interpretation of individual molar types is not feasible in the present study. The *Paranthropus* tooth is the largest (L 338/X-34: 234.32 mm²), but it does not form its own cluster. A more complex picture for upper molars is supported by research on other hominin samples. Moggi-Cecchi and Boccone (2007), in a study on South African hominins, found that *P. robustus* shows a marked relative expansion of the mesial cusps from the first to third molars, and in relation to *Au. africanus* shows different patterns of relative cusp areas depending on which of the three upper molars are compared; this is despite overall similar tooth size. Similarly, Bailey (2004) found distinct cusp area patterns in Neandertals and anatomically modern

507 humans, although this analysis was limited to upper first molars (Neanderthals having a smaller metacone
508 and larger hypocone). Therefore, while such analysis may aid in assessing the phylogenetic placement of
509 Omo upper molars with larger sample sizes, the current limited sample size of upper molars does not
510 allow for assignment of individual Omo teeth (or alignment with other techniques).

511

FIG. 21. – Cluster dendrogram for mandibular molars. The optimal number of clusters has been identified (using the silhouette method), split by cusp area data for either all cusps (left) or the four main cusps (right). All cusps, optimal number of clusters: two; Four main cusps, optimal number of clusters: three. The symbol number on the left represents the genus classification, and the second symbol on the right, if there is one, indicates the predicted genus based on the species classification when different from the genus prediction.

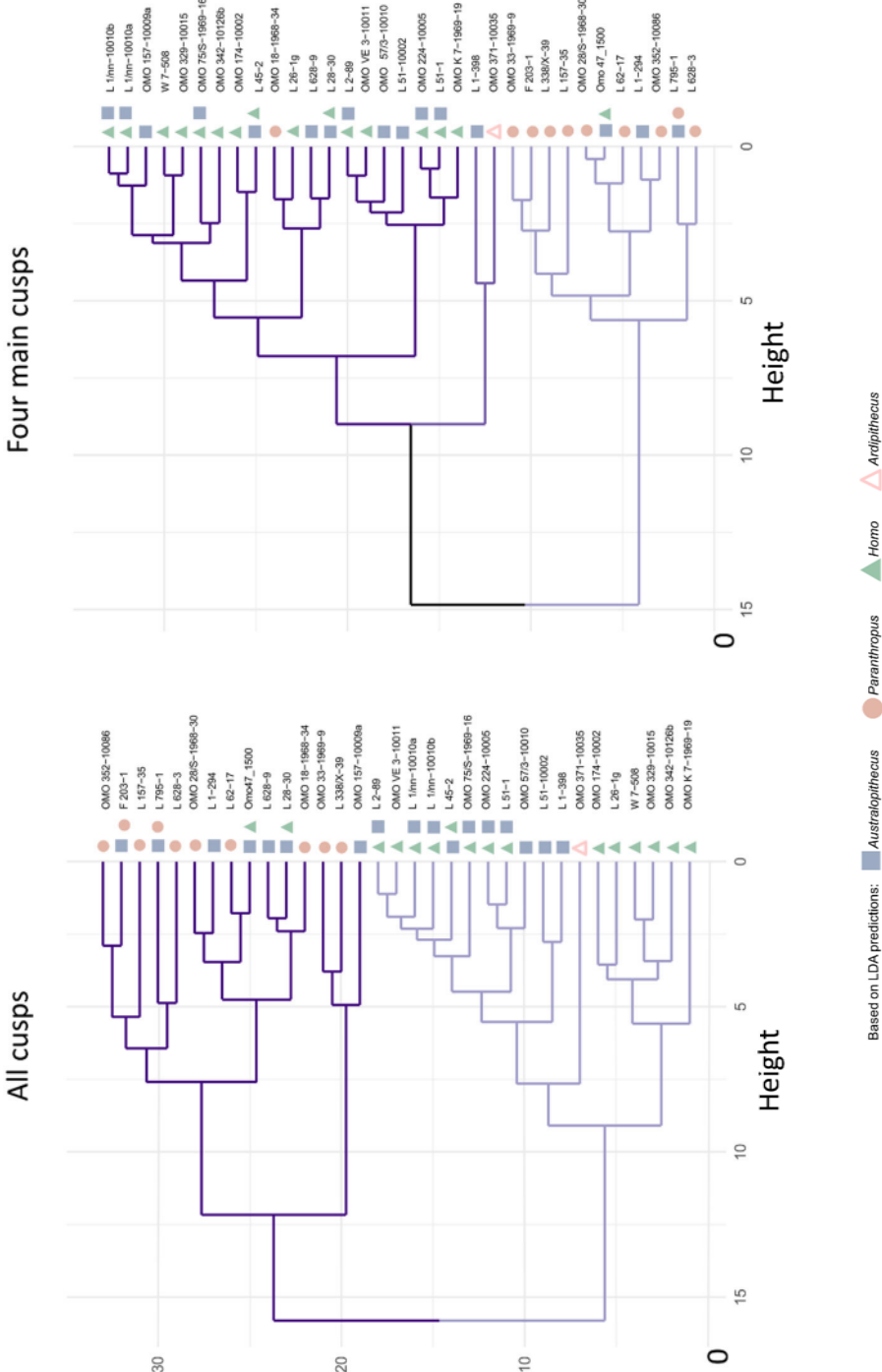
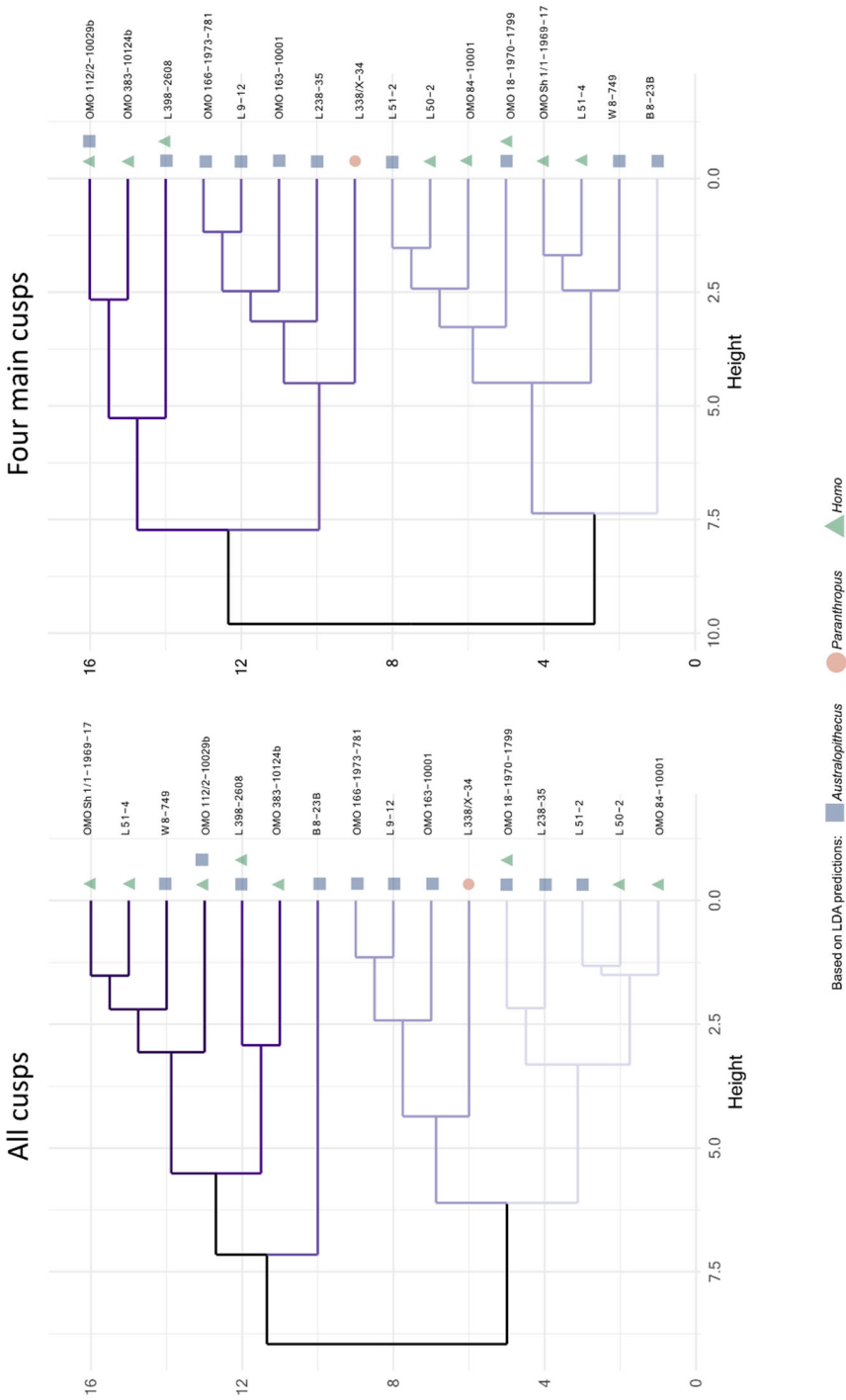


FIG. 22. – Cluster dendrogram for maxillary molars. The optimal number of clusters has been identified (using the silhouette method), split by cusp area data for either all cusps (left) or the four main cusps (right). All cusps, optimal number of clusters: four; Four main cusps, optimal number of clusters: five. The symbol on the left represents the genus classification, and the second symbol on the right, if there is one, indicates the predicted genus based on the species classification when different from the genus prediction.



TAXONOMIC DIFFERENTIATION IN THE COMPARATIVE DATA

Our comparative data show considerable overlap in size, shape ratios, and the LD1 and LD2 plots of *Australopithecus* and *Homo* for all teeth. The over-arching conclusion reached from our analysis of the comparative data is that isolated hominin teeth that plot within this taxonomic overlap cannot be attributed to a specific species. This lack of clear differences between the dentitions of early *Homo* and *Australopithecus* has been noted by other researchers (e.g., Kimbel and Villmoare 2016; Brasil *et al.* 2020; Irish and Grabowski 2021). Given this result, we employ an informal taxonomic category that encompasses specimens that fall into this intermediate morphospace: *Australopithecus* LP/*Homo* EEA. This taxonomic cluster was referred to as “non-robust” by Suwa *et al.* (1996), however, several newly discovered taxa make that category less clear now, such as *Au. garhi* and *Ardipithecus*, both of which are non-robust but not part of the *Australopithecus* LP/*Homo* EEA overlap group.

Our comparative dataset for *P. aethiopicus* is quite limited. To date, Omo sediments are the only to yield fossil evidence of the dentition of *P. aethiopicus* (save for KNM-WT 17000 from west Lake Turkana that preserves only a partial molar and a left P⁴, Walker *et al.* 1986; and see Suwa 1989). There are only 13 specimens (16 teeth) for *P. aethiopicus* available for our comparative dataset, and these are only mandibular (Tables 3 and 4). Aside from the P⁴ and broken maxillary molar of KNM-WT 17000 (Leakey & Walker 1988; for tooth position identification we follow Suwa 1989), we do not have examples of the maxillary teeth of *P. aethiopicus*, in large part because Suwa *et al.* (1996) focused their analysis on the mandibular dentition. However, even with this limited comparative sample, we do see in the LDA that *P. boisei* is distinct from the other taxa, and that *P. aethiopicus* is either intermediate between *P. boisei* and the *Australopithecus* LP/*Homo* EEA group or within the range of variation of *P. boisei*. This is not surprising given that *P. aethiopicus* is widely considered an evolutionary precursor to the more robust species *P. boisei*, likely the phyletic intermediary between *Au. afarensis* and *P. boisei* (Grine 1988; Alemseged *et al.* 2002; Constantino and Wood 2007). For our study here, we identify isolated teeth to *P. boisei*, *P. aethiopicus*, or to *Paranthropus* without the species designation when the overlap between the two species prohibits being more specific.

For some teeth, especially P³, M², and M³, in combination with the morphology (quantitative and qualitative), we can confidently assign some specimens to *Homo* and/or *H. erectus*. Therefore, we also include *Homo* and *H. erectus* in our final taxonomic identifications for the Omo specimens.

The discovery of *Au. garhi* presents an uncomfortable conundrum. There is only one specimen with dentition known for this taxon, BOU-VP-12/30 from the Middle Awash study area in the Afar of Ethiopia. This specimen is a maxillary dental arcade dating to approximately 2.5 Ma (Asfaw *et al.* 1999). BOU-VP-

12/30 has very large post canine teeth, a feature that at first glance aligns it with the robust hominin taxa. We see this in our comparative analyses (Figs. 9-13) and the LDA, as the P^3 , P^4 , M^1 , and M^3 of *Au. garhi* plot well within the morphospace of *P. boisei* (Fig. 14-18). However, the type specimen shows that *Au. garhi* lacks the reduced anterior dentition that characterizes *P. boisei* and robust hominins from South African deposits (Asfaw *et al.* 1999). Given that *Au. garhi* is differentiated from other hominin species by the combination of gracile tooth proportions coupled with very large teeth, isolated teeth do not provide information about *Au. garhi*'s most diagnostic dental feature. A close look at our LDA shows that *Au. garhi* plots within the LD1 and LD2 ranges of *P. boisei* for all post canine teeth except for the M^2 (Fig. 17). This M^2 plots closest to *Australopithecus* LP (Fig. 17), an association that may be primarily driven by the MD dimension (see Fig. 12a). However, without more comparative fossils of *Au. garhi*, we must be resigned to the fact that we are unable to identify this taxon from individual teeth. Therefore, we acknowledge that specimens we attribute to *Paranthropus*, and, at least for the M^2 , that we attribute to *Australopithecus* LP, may actually belong to *Au. garhi*.

In summary, based on our analysis of the comparative data and consideration of morphological variation, we can confidently identify four major taxonomic categories for the isolated Omo teeth: *Australopithecus* LP, *Australopithecus* LP/*Homo* EEA, *Paranthropus* (sometimes to species), and *Homo* (sometimes to *H. erectus*).

DESCRIPTIONS AND TAXONOMIC IDENTIFICATIONS BY STRATIGRAPHIC LEVEL

In this section, we combine the morphological descriptions for each tooth with the results of our LDA predictions (Table 8 and Figures 14-18) and a consideration of the linear metric comparative data (Supplemental Table S1 and Figures 4-13). No one type of analysis nor any one morphological trait can clearly differentiate hominin taxa over this time period. Therefore, our fourth step in the analysis is to apply a thoughtful amount of paleoanthropological "common sense" to which taxonomic categories we assign each tooth (see the Morphological Descriptions section of the Methods for details). As you will see in the text that follows, when the metric and/or morphological features are incongruent or ambiguous, we explain our reasoning for valuing one higher than the other in order to make a final taxonomic determination. Our aim is to provide the transparency needed for the reader to understand our justification for our taxonomic assignment for each specimen, even if the reader does not agree with it.

Usno Formation (3.33 Ma to 3.23 Ma)

Ten specimens derive from Unit U-12 of the Usno Formation. This level corresponds to B-2 of the Shungura Formation. Eight of these specimens are attributed to *Australopithecus* LP and two to *Australopithecus* LP/*Homo* EEA (Table 2).

B 7-39 consists of a left P⁴ (B 7-39B) and a left P³ (B 7-39A) (Howell & Coppens 1974). For B 7-39A, the P³, the MD measurement plots within the first stdv of *H. erectus*, at the lower end of the range of variation observed for *Australopithecus* LP and *Homo* EEA and with the largest specimen of *Ar. ramidus* (Fig. 9A). The BL dimension plots within the first stdv of *Australopithecus* LP, *Au. anamensis*, and at the larger end of the range observed for *Homo* EEA and *H. erectus* (Fig. 9B). The MDxBL size is within the first stdv of *Australopithecus* LP, *Homo* EEA, and *H. erectus*, and among the largest specimens of *Ar. ramidus* (Fig. 9C). The shape index (MD/BL) plots among the smallest specimens of *Australopithecus*, not overlapping with the first stdv of any of our comparative taxa (Fig. 9D). The MD measurement of the P⁴ plots within the first stdv of *Australopithecus* LP, *Au. anamensis*, and *Homo* EEA; BL plots within the first stdv of *Au. anamensis*; MDxBL plots in the first stdv of *Au. anamensis* and among the larger specimens of *Australopithecus* LP; and the size ratio (MD/BL) plots within the first stdv of *Au. anamensis*, *Au. deyiremeda*, and *H. erectus*, and just below that of *P. boisei* (Fig. 10). Our LDA assigns the P³ to *Homo* (44% likelihood) and *Australopithecus* LP (37% likelihood), and the P⁴ to *Australopithecus* (75% likelihood) and *Australopithecus* LP (58% likelihood) (Table 8). On the LDA plot, the P⁴ of B 7-39 is in the center of the *Australopithecus* LP polygon, without overlap of the *Homo* EEA polygon (Fig. 15). The P³ is also within the *Australopithecus* LP polygon, but also within the polygons of *Ar. ramidus*, *Au. anamensis*, *Homo* EEA, and *H. erectus* (Fig. 14). B 7-39B shows a mesial accessory ridge, an interrupted transverse crest and a bifurcated buccal essential crest, but only a single lingual one. The mesiobuccal quadrant of this P³ (in occlusal view) is slightly extended, as has been described as common to *Au. afarensis* (Asfaw *et al.* 1999). As for the characters considered in cladistic analyses, only character 6 applies (Table 6), and this aligns B 7-39 with *Australopithecus* and *Homo* compared to *Ardipithecus*. In comparison to fossils within the hypodigm of *Au. afarensis*, the P³ is a close match to the same tooth in palate A.L. 200-1a, although less worn (see figure in Johanson & White 1979). The P⁴ is morphologically similar to the P⁴ of A.L. 200-1a but a little larger and a little rounded in the occlusal outline, being more similar in morphology to A.L. 333-2. Considering the totality of the evidence, we assign this specimen to *Australopithecus* LP (Table 2).

B 8-14B and **B 8-4Q** are both P⁴s (Howell & Coppens 1974) with linear dimensions that are very similar to each other (Fig. 10). Their univariate dimensions both plot within the first stdv of *Australopithecus* LP and either within or close to *Homo* EEA for all four metric parameters (MD, BL, MDxBL, and MD/BL), and

within the first stdv of *Au. anamensis* for MD, MDxBL, and MD/BL. For the size ratio, they plot within the overlap of all taxa save for *Ar. ramidus*, *Au. garhi*, and *P. aethiopicus*. The LDA predicts B 8-14B to be *Australopithecus* (53%) and *Australopithecus* LP (53%), and B 8-4Q to be *Australopithecus* (56%) and *Australopithecus* LP (54%) (Table 8). On the LDA plot, these two premolars plot very close to each other, and both are near the center of the *Australopithecus* LP polygon, overlapping with the *Homo* EEA polygon (Fig. 15). While the occlusal surface of B 8-14B is too worn for accurate scoring, the central groove separates the lingual and buccal cusps with no evidence of a continuous transverse crest. For cladistic character 6, both specimens align with *Australopithecus* and *Homo* rather than *Ardipithecus* (Table 6). B 8-4Q is essentially unworn, shows mesial and distal accessory ridges, a small accessory cusp at the distal end of the sagittal groove, and a single buccal essential crest but a bifurcated lingual one. B 8-4Q is a slightly larger and less worn version of the left P⁴ of A.L. 200-1 (see figure in Johanson & White 1979). B 8-14B is similar in wear and shape to the left P⁴ of A.L. 333-2. However, the distolingual aspect of the Hadar specimen is more squared compared to the more rounded aspect of the Omo specimen. Coppens (1980) assigned B 8-14 to *Australopithecus* sp. We conclude that *Australopithecus* LP is the most supported identification for both of these premolars (Table 2).

B 8-23 is an associated P⁴ (B 8-23A) and M³ (B 8-23B) (Howell & Coppens 1974). The P⁴ plots within the first stdv of *Au. deyiremeda* for all four linear metric parameters (Fig. 10). The M¹ linear dimensions plot within the first stdv of *Australopithecus* LP and *Au. anamensis* for MD, BL, MDxBL, and just below the first stdv for the shape index, within the first stdv of *Ar. ramidus* (Fig. 11). The LDA predictions (Table 8) assign the P⁴ to *Homo* (50%) and *H. erectus* (42%), and the M³ to *Australopithecus* (44%) and *Australopithecus* LP (33%). When plotted on the LD1 and LD2 axes, the P⁴ (B 8-23A) is within the overlap of three polygons: *Australopithecus* LP, *H. erectus*, and *Au. deyiremeda* (Fig. 15). The LD1 and LD2 values for M³ plot within the overlap of the polygons for *Ardipithecus*, *Australopithecus* LP, *Au. anamensis*, *H. erectus*, and also *Homo* EEA (Fig. 18). Nothing about the morphology precludes an assignment to *Australopithecus*. B 8-23A presents mesial and distal accessory ridges, an interrupted transverse crest and a marked groove on the disto-buccal surface. Both buccal and lingual essential crests are bifurcated. B 8-23B exhibits a weak metacone, a large hypocone and a continuous oblique crest. The mesiobuccal cusp is broken but in the mesiolingual one we can observe a groove as a Carabelli's trait. The P⁴ has the occlusal outline of L.H. 22-a, but is much less worn. This P⁴ is also quite similar to A.L. 200-1 in terms of occlusal outline and the mesial and distal foveae. The molar (B 8-23B) has a diminutive distobuccal cusp that gives it the appearance of an M³. The mesial wear facet does not match the wear facet on the P⁴ (indicating that it is not an M¹), and it lacks a distal wear facet that should be there if this were an M². The B 8-23 M³ is very

similar in size, shape, and cusp proportions to the M³ A.L. 161-40. Coppens (1980) assigned B 8-23 to *Australopithecus* sp. We conclude that *Australopithecus* LP is the most appropriate identification for this specimen (Table 2).

W 7-23 is a P₄ (Howell 1969; Howell & Coppens 1974). The morphology of the crown is asymmetrical with cusp placement and talonid size indicative of a non-robust hominin. In terms of univariate linear metric size, this crown plots well within the overlap of *Australopithecus* and *Homo* EEA (Fig. 5). The shape index is among the highest values observed for *Australopithecus* LP and *P. boisei* (Fig. 5D). The LDA predicts this crown to be *Australopithecus* (79%) and *Australopithecus* LPD (70%) (Table 8). On the LDA plots, W 7-23 is at the edge of the *Australopithecus* LP polygon, close to but just outside the polygon of *Homo* EEA (Fig. 15). In terms of size, shape, and wear, this crown is a close match to A.L. 333w-1. We conclude that *Australopithecus* LP is the best supported identification (Table 2).

W 7-508 is a right M₁ (Howell 1969; Howell & Coppens 1974; Suwa 1996). The linear metrics of this tooth plot in the overlapping ranges of *Australopithecus* and *Homo* (Fig. 6A-C). For the shape index, this crown plots in the overlapping ranges of *Ar. ramidus*, *Au. afarensis*, *Au. anamensis*, *Homo* EEA, *H. erectus*, and *P. boisei* (Fig. 6D). Morphologically, the crown is essentially unworn. W 7-508 has the *Dryopithecus* Y-groove pattern and shows a pronounced anterior fovea with an interrupted middle and distal trigonid crest. This crown also has an L-shape deflecting wrinkle that contacts the hypoconid. The hypoconulid is large and centrally placed. There is a protostylid that extends across most of the buccal surface of the protoconid. The LDA prediction is *Homo* (71%) and *Homo* EEA (36%) (Table 8). On the LDA plot, W 7-508 is in the center of the overlapped regions of the *Australopithecus* LP, *Homo* EEA, *H. erectus*, *Au. anamensis*, and *Au. deyiremeda* polygons (Fig. 16). Overall, the MD, BL, MDxBL, and MD/BL dimensions match most closely with OH 6, a specimen categorized as *Homo* EEA, however, it is also very similar to LDD-VP-1/672 and LH 4, both *Au. afarensis*. W 7-508 is a fairly close match in size, shape, and wear to L.H. 3t, although the Laetoli specimen has a less pronounced protoconid shelf. Given the ambiguity between *Australopithecus* LP and *Homo* EEA, we classify this specimen as *Australopithecus* LP/*Homo* EEA (Table 2).

W 8-749 is an isolated right maxillary M¹. W 8-749 was initially identified as a right M² (Howell 1969; Howell & Coppens 1974). We find the morphology much more aligned with that of a right M¹ and therefore analyze it as such. W 8-749's MD dimension plots within the first stdv of *Australopithecus* LP, *Homo* EEA, and *H. erectus*, whereas the BL dimension only overlaps with the larger values attributed to *Australopithecus* LP (Fig. 11A,B). Consequently, the MDxBL dimension is within the first stdv of *Australopithecus* LP but only plots among the largest individuals attributed to *Homo* EEA and *H. erectus* (Fig. 11C). The LDA predicts the genus to be *Australopithecus* (66%) and the species as *Australopithecus*

LP (46%) (Table 8). On the LDA plot, W 8-749 is centered in the *Australopithecus* LP polygon, overlapping with the *Homo* EEA and the *Au. anamensis* polygons (Fig. 16). The crown is moderately worn with no dentine exposed. In cusp proportions, arrangement, and size, this fossil is most like L.H. 21a, although the Omo specimen is a little more worn on the occlusal surface. We conclude that *Australopithecus* LP is the most appropriate identification (Table 2).

W 8-752 is a worn right M₁ (in agreement with Howell 1969, and Howell & Coppens, 1974; disagreeing with the designation as M₂ by Suwa 1996). This is a moderately worn crown with a small amount of dentine exposed on the hypoconid. The mesiobuccal aspect is worn away, but enough remains to measure the MD dimension with enough confidence to make comparisons. The linear metric dimensions of this tooth plot within the first stdv of *Australopithecus* LP and *Homo* EEA for MD and MDxBL, and with these two taxa and *H. erectus* for BL (Fig. 6A-C). The shape index plots in the upper ranges of *Australopithecus* LP, *Au. anamensis*, *H. erectus*, and *P. boisei*, and within the first stdv of *Homo* EEA (Fig. 6D). The LDA results predict this tooth to belong to genus *Homo* (68%) and *Homo* EEA (43%) (Table 8). However, it plots well within in the overlap zone of *Au. LP* and *Homo* EEA (Fig. 16). Morphologically, this molar has the five main cusps, including a large hypoconulid. The groove pattern appears to be cruciform, but this is difficult to be certain about since the crown is fairly worn. The crown is similar to W 7-508, although worn fairly flat. In comparison to *Au. afarensis* specimens, this tooth is similar in size, cusp proportions, and cusp arrangement to A.L. 333-74, although the Hadar specimen is much more worn. This tooth is also similar in morphology to MAK-VP-1/12, although the Omo specimen is slightly larger. Given the similarity to W 7-508, we include this specimen in the *Australopithecus* LP/*Homo* EEA group (Table 2).

W 8-988 is a left P⁴. The linear dimensions plot at the first stdv of *Au. anamensis* and among the largest individuals observed in *Australopithecus* LP and *Homo* EEA (Fig. 10A-C). The shape index is similar to that of B 8-4Q, plotting within the first stdv of *Australopithecus* LP, *Au. anamensis*, and *Homo* EEA (Fig. 10D). Our LDA prediction is *Australopithecus* (82%) and *Australopithecus* LP (58%) (Table 8). On the LDA plot, W 8-988 is in the center of the *Australopithecus* LP distribution, just at the edge of the *Homo* EEA polygon (Fig. 15). Morphologically, this crown is very similar to that of B 8-23A, though much larger in size. In comparison to *Au. afarensis*, W 8-988 is similar to A.L. 333x-42, but less worn. We conclude that *Australopithecus* LP is the most supported identification (Table 2).

W-978 is a right P₃ with linear dimensions and a shape index that plots within the overlap of *Australopithecus* LP, *Homo* EEA, and *H. erectus* (Fig. 4A-D). The LDA prediction is *Australopithecus* (54%) and *Australopithecus* LP (54%) (Table 8). On the LDA plot, W-978 is located within a dense cluster of comparative specimens assigned to *Australopithecus* LP and *H. erectus* (Fig. 14). There is a moderate

mesiobuccal protrusion of the crown base that aligns it more with *Ar. ramidus*, *Au. anamensis*, and *Au. afarensis*. In terms of size, shape, and cusp proportions, W-978 looks like an unworn version of A.L. 207-13. We assign this tooth to *Australopithecus* LP (Table 2).

Upper units of Member B (B-9, B-10, and B-12, from 3.03 Ma to 2.94 Ma)

There are ten specimens from the upper levels of Member B. We assign five specimens to *Australopithecus* LP/*Homo* EEA, two to *Australopithecus* LP, and three to *Paranthropus* or cf. *Paranthropus* (Table 2).

L 1/nn-10010a and L 1/nn-10010b are M₂ antimeres, a is from the right; b is from the left. They both exhibit the Y-groove pattern and an anterior fovea. The hypoconulid and entoconulid are almost equal in size, and each is smaller than the hypoconid. The linear dimensions plot closely to L 1-398, overlapping mostly with the variation observed in *Australopithecus* LP and *Homo* EEA (Fig. 7). The LDA predictions are *Homo* (55% for both crowns) and *Australopithecus* LP (45% for the right and 46% for the left) (Table 8). On the LDA plot, these two teeth plot very close to each other, and both are in a dense cluster of specimens from *Australopithecus* LP, *Homo* EEA, and *H. erectus* (Fig. 17). The cusp configuration of these two crowns is like A.L. 207-13 and A.L. 241-14, although the Omo specimens are larger than both. The L 1/nn-10010 specimens are more similar in size to A.L. 333w-60. We conclude that the most appropriate taxonomic category is *Australopithecus* LP /*Homo* EEA (Table 2).

L 1-294 is a right M₃ (Howell & Coppens 1974; Suwa *et al.* 1996). The MD, BL, and MDxBL dimensions plot at the lower end of the range of variation observed for *P. boisei* and in the upper ranges of *Australopithecus* and *Homo* EEA (Fig. 8A-C). The LDA predictions are *Australopithecus* (74%) and *Australopithecus* LP (49%), and it plots right in the middle of the overlap zone of the *Paranthropus*, *Australopithecus* LP, *Au. anamensis*, and *Homo* EEA polygons (Fig. 18). Suwa *et al.* (1996) designated this tooth to *Australopithecus*/*Homo* gen. and sp. indet. However, the morphology of this crown is almost identical to OMO 28/S-1968-30 and very similar to L 795-1, both assigned to *Paranthropus* (Table 2). Like OMO 28/S-1968-30, L 1-294 exhibits a double entoconulid, although more moderate in size. L 1-294 also has a large hypoconulid and a cusp-shaped protostylid (type 6 in Hlusko 2004). In comparison to *Au. afarensis*, this crown is most similar to MAK-VP-1/4, although the Omo specimen is slightly larger with a proportionately larger hypoconulid and smaller hypoconid. In our opinion, despite the linear dimensions of this crown being aligned with *Australopithecus*, we conclude that L 1-294 is best categorized as cf. *Paranthropus* (Table 2).

L 1-398 is a right M_2 (Suwa *et al.* 1996, identify this crown as an M_3). Morphologically, this crown has the *Dryopithecus* Y-groove pattern, a mesial marginal ridge that is continuous and thin, a slight anterior fovea, and an interrupted middle and distal trigonid crest. The protoconid displays a strong protostylid and the metaconid exhibits a well-developed deflecting wrinkle. The entoconid is very small, and the crown has a very small C5 and C6. The linear dimensions may be slightly under-valued, as the cervical margin of the crown is missing. With this caveat in mind, all dimensions plot very close to the mean of *Australopithecus* LP, with some overlap with other taxa (Fig. 7A-C). The shape index overlaps with the first stdv of *Australopithecus* LP, *Au. anamensis*, *Homo* EEA, *H. erectus*, and *P. boisei* (Fig. 7D). The LDA predictions are *Australopithecus* (49%) and *Australopithecus* LP (52%) (Table 8). In the LDA plot, L 1-398 is among a dense cluster of *Australopithecus* LP, *Homo* EEA, and *H. erectus* (Fig. 17). Even though Suwa *et al.* (1996) identify this crown as an M_3 rather than as an M_2 , they come to a similar conclusion as to the taxonomy, identifying it as *Australopithecus/Homo* gen. and sp. indet. We designate this tooth as *Australopithecus* LP/*Homo* EEA (Table 2).

L 2-89 is a left M_3 (Howell & Coppens 1974; Suwa *et al.* 1996). Morphologically, it is a fairly worn crown. Because the crown is worn flat on the buccal cusps but no dentine is exposed, we assume that the enamel is relatively thick. The mesiolingual aspect is mostly unworn while the distal part is worn flat, which is more characteristic of *Australopithecus* than *Paranthropus*. The molar exhibits a pronounced anterior fovea with discontinuous middle and distal trigonid crests. Although there is distobuccal wear, the contours of the cusps allow us to perceive a large hypoconulid and a moderate entoconulid. The linear dimensions plot among the smaller specimens of *Australopithecus* LP and *Homo* EEA, within the first stdv for MD (Fig. 8A), and within or close to the first stdv of *Ar. ramidus* and *H. erectus* for BL and MDxBL (Fig. 8B,C). In terms of the shape ratio, L 2-89 plots within the large overlap zone across taxa, but falls within the first stdv of *Homo* EEA and *P. boisei* (Fig. 8D). The LDA prediction is *Homo* (63%) and *Australopithecus* LP (33%) (Table 8). On the LD1 versus LD2 plot, L 2-89 plots in the *Australopithecus* LP polygon just within the overlap with the *Homo* EEA polygon (Fig. 18). Despite the LDA affinity to *Homo*, the morphology of this crown, and in particular the extended hypoconulid, is more similar to *Australopithecus*. L 2-89 is similar in size to A.L. 288-1 ("Lucy"), but the Omo specimen has a more rectangular distal aspect. We conclude that the most appropriate taxonomic assignment is *Australopithecus* LP/*Homo* EEA (Table 2). Similarly, Suwa *et al.* (1996) also assigned this tooth to *Australopithecus/Homo* gen. and sp. indet.

L 795-1 is a right M_3 . Suwa (1996) identified this crown as an M_2 ; we interpret the rounded distal aspect of the crown to be more reminiscent of an M_3 . L 795-1 has a thick mesial marginal ridge that encloses a pronounced linear anterior fovea. The middle and distal trigonid crests are continuous and the essential

crest of the metaconid is slightly deflected. There is a small hypoconulid and metaconulid, and one entoconulid. The cusps are relatively more rounded and bulging compared to others from this stratigraphic level. The MD and BL dimensions plot with the smaller specimens of *Paranthropus* and the largest specimens of *Australopithecus* and *Homo* EEA (Fig. 8A and B). However, the MDxBL value is outside the *Australopithecus* and *Homo* ranges, and just at the lower edge of the first stdv of both *P. aethiopicus* and *P. boisei* (Fig. 8C). The shape index plots in the first stdv of *Ar. ramidus* and *H. erectus*, and in the lower range of variation for *Australopithecus* LP, *Au. anamensis*, *Homo* EEA, and *P. boisei* (Fig. 8D). The LDA predicts *Australopithecus* (57%) and *P. boisei* (49%) (Table 8). This tooth was previously given an indeterminate taxonomic categorization (Howell & Coppens 1974; Suwa *et al.* 1996). We are more specific and assign this to *Paranthropus* (Table 2).

OMO 28/s-1968-30 is a right M₃ previously given an indeterminate taxonomic categorization (Howell & Coppens 1974; Suwa *et al.* 1996). The crown is rounded with bulging buccal cusps that are lingually oriented, a characteristic of *Paranthropus* (character 3, Table 6). The occlusal surface has the Y-groove pattern and exhibits a double entoconulid. OMO 28/S-1968-30 has a medium-sized hypoconulid, a small metaconulid and a moderately expressed protostylid. The linear dimensions plot at the middle to lower end of the range of variation observed for *P. boisei* and *P. aethiopicus*, only overlapping with the largest *Australopithecus* specimens in its BL breadth (Fig. 8A-C). The shape index is high, plotting at the top of the range of variation observed for *P. aethiopicus* and *Homo* EEA, the taxa with the highest shape indices (Fig. 8D). The LDA predictions are *Paranthropus* (85%) and *P. aethiopicus* (62%) (Table 8). On the LDA plot, this specimen plots in a cluster of *P. boisei* and *P. aethiopicus* in our comparative sample, close to the overlap with the *Australopithecus* LP polygon but distinct (Fig. 18). We conclude that *Paranthropus* is the most appropriate taxonomic category (Table 2).

OMO 112/2-10029 is comprised of two isolated teeth (a and b) found within the same square meter. OMO 112/2-10029b is a right M³ that has a small metacone and hypocone, a small cuspule as a metaconule, and a Carabelli's cusp in a large Y-shape. The MD dimension overlaps with the first stdv of *Ar. ramidus* and *H. erectus*, and among the smallest specimens of *Australopithecus* LP, *Au. anamensis*, and *Homo* EEA (Fig. 13A). The BL dimension and the MDxBL size plot among the smallest specimens of *Ar. ramidus*, *Australopithecus* LP, *Au. anamensis*, and *Homo* EEA, and within the first stdv of *H. erectus* (Fig. 13B,C). The shape ratio (MD/BL) is within the first stdv of *Australopithecus* LP, *Au. anamensis*, and *H. erectus* (Fig. 13D). The LDA predication for the M³ are *Homo* (43%) and *Australopithecus* LP (29%) (Table 8). It plots on the LDA graph in the overlap between the *Australopithecus* LP, *Ar. ramidus*, and *H. erectus* polygons, very close to the *Au. anamensis* and *Homo* EEA polygons (Fig. 18). OMO 112/2-10029a is a right

lower M₂ that exhibits the Y-groove pattern with a strong cusp 5. The LDA predictions for this M₂ are *Australopithecus* (54%) and *Australopithecus* LP (53%) (Table 8). On the LDA graph, like for the M³, this tooth plots in a cluster of comparative specimens from *Australopithecus* LP, *H. erectus*, *Homo* EEA, and *Au. anamensis* (Fig. 17). The mis-match in taxonomic predictions for these two teeth is likely a reflection of the inability for linear dimensions and combinations thereof to differentiate taxa with high confidence (especially for M₂, see Table 9 and associated discussion); however, it is also possible that these two teeth derive from different individuals. For now, we consider them as the same individual and conclude that they are most appropriately placed into our category of *Australopithecus* LP/*Homo* EEA (Table 2).

OMO 112/4-10009 is a left P³ with strong affinities to *Australopithecus* LP in terms of metric size, proportions, and crown morphology. The crown is less worn than B 7-39A and is slightly larger, but the overall shape is very similar. The linear MD dimension overlaps with the first stdv of *Australopithecus* LP and *Homo* EEA; BL plots with the larger specimens of *Australopithecus* LP, *Au. anamensis*, and *Homo* EEA (Fig. 9A,B). The LDA predictions are *Australopithecus* (54%) and *Australopithecus* LP (43%) (Table 8). The LDA plot places this tooth within a dense cluster of comparative specimens of *Australopithecus* LP, *H. erectus*, *Homo* EEA, and *Au. anamensis* (Fig. 14). The crown is asymmetrical. The mesiobuccal quadrant is extended, as is characteristic of *Au. afarensis* compared to *Homo* (Asfaw *et al.* 1999). This crown is a good match in terms of size, shape, and morphology with L.H. 3-f. We conclude that the most appropriate taxonomic assignment is *Australopithecus* LP (Table 2).

OMO 212-1973-1950 is a lower M₁ germ (Howell & Coppens 1974; Suwa *et al.* 1996) with crenulations and a protoconid shelf (score of 5 as per Hlusko 2004). This crown exhibits the primitive Y-groove pattern, and has a continuous middle and discontinuous distal trigonid crest with a pronounced anterior fovea. The hypoconulid is equal in size to the entoconid. It also has a small protostylid. Suwa *et al.* (1996) designated this crown as *Australopithecus*/*Homo* gen. and sp. indet. Our LDA predictions are *Homo* (80%) and *H. erectus* (39%) (Table 8). This designation is likely driven by the relatively small size of this specimen, whose linear dimensions plot among the smallest specimens of *Au. anamensis* and *Homo erectus*, and either among the smallest specimens or just below the range of observed variation for *Australopithecus* LP and *Homo* EEA (Fig. 6). However, this is a tooth germ and therefore the dimensions likely do not reflect the full size. The shape index overlaps with the range of variation observed for *Australopithecus* LP and *Paranthropus*, but just barely (Fig. 6). OMO 212-1973-1950 plots closer to the first stdv of the *Homo* EEA shape index, and among a cluster of four specimens attributed to *H. erectus* (Fig. 6D). When viewed on the LDA plot, this specimen is in a dense cluster of comparative specimens from *Australopithecus* LP, *H. erectus*, *Au. deyiremeda*, and *Au. anamensis*, and is very close to the *Homo* EEA and *Ar. ramidus* polygons

(Fig. 16). OMO 212-1973-1950 has similar occlusal crenulations, cusp proportions, and cusp arrangement to L.H.-2, but the Omo specimen is much smaller. Weighing the morphology over the size, we conclude that the most appropriate taxonomic category is *Australopithecus* LP/*Homo* EEA (Table 2).

OMO 212-10012 is a right P⁴ with linear dimensions that plot alongside B 7-39B and close to W 8-988, two other P⁴s from Level B that have been assigned to *Au. afarensis* (Table 2). This crown shows a mesial but not distal accessory ridge, a marked groove on the distobuccal surface, and a single lingual essential crest and a bifurcated buccal one. The transverse crest is interrupted by the sagittal fissure. The LDA predictions are *Australopithecus* (77%) and *Australopithecus* LP (57%) (Table 8). The LDA plot shows OMO 212-10012 to be in a cluster of three specimens that includes B 7-39B (Fig. 15; this specimen is unlabelled in the figure; the values are LD1 = 0.42; LD2 = 1). All three of these specimens are in the center of the *Australopithecus* LP polygon, between the overlap with the *Homo* EEA and *Au. anamensis* polygons. Combining the strength of the LDA predictions, the morphology and similarity of this crown to B 7-39 (that has two associated teeth, and therefore more evidence to link it to *Australopithecus* LP), and that it is very similar to the *Au. afarensis* specimen A.L. 333-2 (but with less wear), we assign OMO 212-10012 to *Australopithecus* LP (Table 2).

Member C (2.94 Ma to 2.53 Ma)

There are 22 specimens from Member C, including the five *P. aethiopicus* included in our comparative dataset. In total, 15 are assigned to *Australopithecus* LP/*Homo* EEA, six are either *Paranthropus* or *P. aethiopicus*, and one is categorized as cf. *Homo* (Table 2). This last specimen derives from an area close to a fault, and may derive from Member F rather than Member C.

L 45-2 is a right M₁ (Howell & Coppens 1974; Suwa 1996; Suwa *et al.* 1996). Morphologically, this crown has an interrupted middle and distal trigonid crest and the primitive Y-groove pattern. It has a large hypoconulid that is almost the same size as the entoconid. There is a strong protostylid across the buccal surface and a continuous and thick mesial marginal ridge. Suwa *et al.* (1996) designated this crown as *Australopithecus*/*Homo* gen. and sp. indet. The metric dimensions plot within, or very close to, the first stdv of *Au. anamensis*, *Australopithecus* LP, *Homo* EEA, and *H. erectus* (Fig. 6). The LDA predictions are *Australopithecus* (50%) and *H. erectus* (43%) (Table 8). On the LD1 versus LD2 graph, L 45-2 plots within a cluster of comparative specimens attributed to *Australopithecus* LP, *Au. anamensis*, *Au. deyiremeda*, *Homo* EEA, and *H. erectus* (Fig. 16). Similar to Suwa *et al.* (1996), we assign this tooth to *Australopithecus* LP/*Homo* EEA (Table 2).

L 51-1 is a left M_1 (Howell & Coppens 1974; Suwa 1996; Suwa *et al.* 1996). The linear dimensions of this crown plot consistently for all four parameters within the first stdv overlap between *Australopithecus* LP and *Homo* EEA (Fig. 6). The wear pattern on the crown is not flat like *Paranthropus*, as the lingual cusps are higher than the more worn buccal cusps. Morphologically, L 51-1 exhibits an interrupted middle and distal trigonid crest and the primitive Y-groove pattern. The anterior fovea is a slight linear depression that is bordered mesially by the continuous and thick mesial marginal ridge. The hypoconulid is bigger than the entoconid, and there is a very small C6. The crown has a protostylid with an expression of 2 to 3 (Hlusko 2004). The LDA predictions are *Homo* (54%) and *Australopithecus* LP (45%) (Table 8). On the LDA graph, L 51-1 plots within a dense cluster of comparative specimens attributed to *Australopithecus* LP, *Homo* EEA, and *H. erectus* (Fig. 16). Suwa *et al.* (1996) designated this crown as *Australopithecus/Homo* gen. and sp. indet. We similarly categorize this tooth as *Australopithecus* LP/*Homo* EEA (Table 2).

L 51-2 is a left M^1 (Howell & Coppens 1974). This is a large tooth. The MD dimension plots within the first stdv of *Homo* EEA and only in the upper ranges of variation of *Australopithecus* LP and *H. erectus* (Fig. 11A). The BL dimension is larger than *Homo*, overlapping with the largest values observed for *Australopithecus* LP and the smallest values of *P. boisei* (Fig. 11B). This combination of dimensions places the size of L 51-2 at the upper most MDxBL values observed for *Australopithecus* LP and *Homo* EEA (Fig. 11C). The shape index plots within the first stdv of *Australopithecus* LP, *Au. anamensis*, and *P. boisei* (Fig. 11D). Morphologically, L 51-2 has a large metacone and hypocone and a small cuspule as a metaconule; there is also a Carabelli's pit and a large distal fovea. The LDA predictions are *Australopithecus* (64%) and *Australopithecus* LP (49%) (Table 8). On the LDA graph, this specimen plots only in the *Australopithecus* LP and *Au. anamensis* polygons (Fig. 16). Given the similarity to the *Homo* EEA MD dimension, and that the LD1 value overlaps with those of *Homo* EEA, we see a strong affinity to both *Australopithecus* LP and *Homo*, and therefore assign this tooth to *Australopithecus* LP/*Homo* EEA (Table 2).

L 51-3 is a left M^2 (Howell & Coppens 1974) of intermediate size. The linear dimensions plot in the overlap of *Australopithecus* LP, *Au. anamensis*, *Homo* EEA, and *H. erectus* (Fig. 12A-C). The size ratio is at the higher end of the *Australopithecus* LP range, and overlaps with the first stdv of *Homo* EEA, *H. erectus*, and *P. boisei* (Fig. 12D). Morphologically, L 51-3 displays a very large metacone, a large hypocone, and distal groove (that is almost erased by wear) separating both cusps. There is a continuous *crista obliqua* and a moderately-sized Carabelli's cusp. The LDA predictions are *Homo* (51%) and *Australopithecus* LP (32%) (Table 8). On the LDA graph, this tooth plots near the center of the *Australopithecus* LP, *Homo* EEA, and *H. erectus* polygons, also overlapping with the polygon of *Au. anamensis* (Fig. 17). We assign this tooth to *Australopithecus* LP/*Homo* EEA (Table 2).

L 51-4 is a left M¹ (Howell & Coppens 1974). The linear dimensions plot at the upper end of the first stdv of *Australopithecus* LP and *Homo* EEA for all three size measurements (MD, BL, MDxBL), and intermediate between *Australopithecus* LP and *Homo* EEA for the shape ratio, within the first stdv of *H. erectus* (Fig. 11). Morphologically, **L 51-4** displays a very large metacone and hypocone, a small cuspule as a metaconule, a continuous *crista obliqua*, and mesial marginal accessory tubercles. L 51-4 also has a Carabelli-like trait in the form of a small Y-shaped depression on the mesiolingual aspect. The LDA predictions are *Homo* (65%) and *H. erectus* (35%) (Table 8). On the LDA graph, this tooth plots near the center of the *Australopithecus* LP and *Homo* EEA polygons, and also plots within *H. erectus* and *Au. anamensis* (Fig. 16). We assign this tooth to *Australopithecus* LP/*Homo* EEA (Table 2).

L 51-79 is a right P₄ included in our analysis as a comparative specimen for *P. aethiopicus*, following the identification by Suwa *et al.* (1996).

L 51-80 is a right P₄ (Howell & Coppens 1974; Suwa *et al.* 1996). The linear dimensions of this crown plot within the overlap of *Australopithecus* LP and *Homo* EEA for all three size parameters, but only with the first stdv of *H. erectus* in the BL dimension (Fig. 5A-C). The size ratio plots in the overlap of all taxa except for *Ar. kadabba* and *Au. anamensis* (Fig. 5D). Morphologically, the cusps are more centrally oriented and the talonid is not as extended as in *Paranthropus*. The LDA predictions are *Australopithecus* (63%) and *Australopithecus* LP (55%) (Table 8). On the LDA graph, L 51-80 plots within a dense cluster of comparative specimens attributed to *Homo* EEA, *H. erectus*, *Australopithecus* LP, *Au. anamensis*, and *Au. deyiremeda* (Fig. 15). Suwa *et al.* (1996) designated this crown as *Australopithecus*/*Homo* gen. and sp. indet. We similarly attribute it to *Australopithecus* LP/*Homo* EEA (Table 2).

L 51-10002 is a right M₃. The linear dimensions overlap with *Australopithecus* LP and *Homo* EEA for all three size parameters (Fig. 8A-C) and the shape ratio (MD/BL) overlaps with all multi-specimen taxa except for *P. aethiopicus* (Fig. 8D). Morphologically, this tooth is worn more similarly to *Australopithecus* than *Paranthropus*, as the lingual cusps are higher than the more-worn buccal cusps. The crown has a Y-groove pattern. The hypoconulid is equal in size to the entoconid. There is also a double C6. There is a cusp-shaped protostylid with an apex that extends independently from the main crown (type 6, Hlusko 2004). The LDA predictions are *Australopithecus* (54%) and *Australopithecus* LP (50%) (Table 8). On the LDA graph, L 51-10002 plots within a dense cluster of comparative specimens from *Australopithecus* LP, *Au. anamensis*, *Homo* EEA, and *H. erectus* (Fig. 18). We assign this crown to *Australopithecus* LP/*Homo* EEA (Table 2).

L 55-33 is a left P₄ in a mandibular fragment. We include this specimen in our comparative sample as *P. aethiopicus* based on the identification and description of Suwa *et al.* (1996).

L 62-17 is a right M₂. We include this specimen in our comparative sample as *P. aethiopicus* based on the identification and description of Suwa *et al.* (1996).

L 220-10001 is a right M³. The metric dimensions of this crown are among the largest specimens of *Australopithecus* LP and *Homo* EEA, and also among the smallest of the *Paranthropus* specimens. In terms of the BL dimension, it is notably similar to the one known specimen of *Au. garhi* (Fig. 13). The shape index plots within the overlap of most of the comparative taxa (Fig. 13D). Morphologically, this crown has relatively very small metacone and hypocone cusps, and numerous tubercles along the mesial marginal ridge, a feature that is more like *Australopithecus* than *Homo*. The LDA predictions are *Australopithecus* (66%) and *Australopithecus* LP (47%) (Table 8). On the LDA graph, L 220-10001 plots within the overlap of the *Australopithecus* LP and *Homo* EEA polygons (Fig. 18, with LD1 = 0.81 and LD2 = -0.9). We classify this tooth as *Australopithecus* LP/*Homo* EEA (Table 2).

OMO 18-1968-31 is a left P₃. We include this specimen in our comparative sample as *P. aethiopicus* based on the identification and description of Suwa *et al.* (1996).

OMO 18-1968-33 is a left P₃ (Howell & Coppens 1974; Suwa *et al.* 1996). This crown is more mesiodistally elongated than any of our comparative specimens, being 0.1mm larger than LH-3 (*Au. afarensis*) in the MD dimension and 0.5mm smaller in the BL dimension. The shape ratio (MD/BL) is slightly lower than ARI-VP-3/80 (*Au. afarensis*). The LDA predictions are *Australopithecus* (53%) and *Australopithecus* LP (50%) (Table 8). On the LD1 versus LD2 plot, OMO 18-1968-33 is closest to the *Australopithecus* LP polygon but just outside of it along the LD1 axis (Fig. 14). On the LD2 axis, this tooth overlaps with the distribution of *Australopithecus* and *Homo* (Fig. 14). Morphologically, this P₃ has strong similarities to OMO 18-1968-31, which has been classified in earlier studies as *P. aethiopicus* (Suwa *et al.* 1996). However, because the BL dimension is so far from the range of variation observed for the *Paranthropus* species but overlaps with the first stdv of *Australopithecus* LP, *Homo* EEA, and *H. erectus*, and because this specimen plots on the opposite extreme of LD1 away from *Paranthropus*, we assign this specimen to *Australopithecus* LP/*Homo* EEA (Table 2).

OMO 18-1968-34 is a left M₁. We include this specimen in our comparative sample as *P. aethiopicus* based on the identification and description of Suwa *et al.* (1996).

OMO 18-1970-1799 is a left M² (originally identified as left M¹, Howell & Coppens 1974). Morphologically, it presents a large metacone and hypocone and a small cusplule as a metaconule. The *crista obliqua* is continuous and there is a notable Carabelli-like cingular remnant on the lingual surface of the protocone. The mesial marginal ridge has little tubercles and the distal fovea is small. The occlusal fovea is relatively closed, giving it a more *Paranthropus*-like appearance (character 3, Table 6). The linear

metrics are large, plotting among the largest specimens of the non-robust taxa and the smallest of the *P. boisei* specimens, similar to that of *Au. garhi* (Fig. 12). The LDA predictions are *Australopithecus* (59%) and *Australopithecus* LP (42%) (Table 8). Interestingly, this crown plots within the *P. boisei* polygon with no overlap with other comparative taxa in LD1, and in a distinctly different LD1 and LD2 space from the one specimen of *Au. garhi* (Fig. 17). LD1 explains 85% of the variance within the comparative data (Table 7), giving this affinity to *P. boisei* a weight we add to the *Paranthropus*-like occlusal foveal morphology already mentioned. With all this in mind, we assign this tooth to *Paranthropus* (Table 2).

OMO 69-1974-900 is a left P⁴. It presents a distal accessory ridge and a weak transverse crest. Both buccal and lingual essential crests are bifurcated. The mesiobuccal corner projects slightly, aligning the morphology with *Australopithecus*. The linear dimensions plot within the first stdv of *Au. deyiremeda* for all dimensions, and either in the overlap between *Homo* EEA and *H. erectus* or just between their distributions (Fig. 10). The LDA predictions are *Homo* (56%) and *H. erectus* (37%) (Table 8). On the LDA graph, this tooth plots in the polygons of *Australopithecus* LP, *H. erectus*, and very close to the polygons of *Au. anamensis* and *Ar. ramidus* (Fig. 15). We conclude that the most appropriate taxonomic assignment is *Australopithecus* LP/*Homo* EEA (Table 2).

OMO 84-10001 is a worn left M¹ with a large metacone and protocone. The crown morphology is simple with a well-developed hypocone that is about equal in size to the distobuccal cusp. The linear dimensions are among the largest specimens of *Australopithecus* LP and *Homo* EEA, and for the MD dimension, the smallest specimens of *P. boisei* (Fig. 11A-C). The shape index of OMO 84-10001 plots within the first stdv of *Homo* EEA and *H. erectus* (Fig. 11D). For M¹, the shape index of *Homo* EEA is statistically significantly different from *Australopithecus* LP (Supplemental Table S7), providing support for a taxonomic assignment of *Homo* for this specimen. The LDA predictions are *Homo* (66%) and *Homo* EEA (43%) (Table 8). The next-highest species prediction is *Australopithecus* LP (30%) (Supplemental Table S9). On the LDA graph, the LD1 and LD2 values for this tooth plot in the center of the *Homo* EEA polygon, but also overlap with the polygons for *Australopithecus* LP and *Au. anamensis* (Fig. 16). This stratigraphic horizon for this specimen is somewhat uncertain as it comes from an area by a fault. There are stone tools typical of Member F on one side of the fault, and on the other side (where the tooth comes from), there are scarce faunal remains to help with the stratigraphic correlation. Therefore, it is tentatively included in Member C. Because of the strong affinity to *Homo*, we assign this specimen to cf. *Homo* (Table 2).

OMO 157-10009 is comprised of five isolated molar fragments that were found in a limited area of the sedimentary outcrop and therefore assumed to be associated. The only complete crown is OMO 157-10009a, a left M₃. Morphologically, the crown is crenulated with a strong protoconid shelf and several

other ancillary crown features. It has the X pattern on the occlusal surface and exhibits an interrupted middle and distal trigonid crest and the Y-groove pattern. OMO 157-10009a has an entoconid and hypoconid equal in size with a hypoconulid larger than either. There is also a C6 with a metaconule. The mesial marginal ridge is continuous and thin. On the buccal surface of the protoconid there is a well-developed protostylid. The linear dimensions fall within the first stdv of *Au. anamensis*, *Australopithecus* LP, and *Homo* EEA (Fig. 8A-C). The shape index similarly overlaps with the first stdv of *Au. anamensis*, *Australopithecus* LP, *Homo* EEA, and also *P. boisei* (Fig. 8D). The LDA predictions are *Australopithecus* (66%) and *Australopithecus* LP (53%) (Table 8). On the LD1 versus LD2 graph, this tooth plots in the center of the comparative specimens, at the apex of the u-shape made by the plotted data. This placement is within the polygons of *Australopithecus* LP, *Au. anamensis*, *Au. deyiremeda*, *Homo* EEA, and *H. erectus*, and very close to the edge of the *P. boisei* polygon (Fig. 18). This is the only lower molar in the *Australopithecus* LP/*Homo* EEA group where the protoconid and entoconid are in contact (X groove pattern). We classify this crown as *Australopithecus* LP/*Homo* EEA (Table 2).

OMO 163-10001 is a right M³ germ. This is a heavily crenulated crown with a large metacone, a small hypocone and a medium-sized metaconule with a secondary distal cusp. This is the only upper molar in the Omo sample with a double metaconule. The mesial marginal ridge displays tubercles, and there is a small distal fovea. The linear metric dimensions, especially the MD dimension, plot among the larger of the non-robust specimens, but have the most overlap with the larger specimens of *Australopithecus* LP (Fig. 13A-C). The shape index is among the highest observed in our comparative sample, most similar to two *Homo* EEA (KNM-ER 1805 and KNM-ER 62000). The LDA predictions are *Australopithecus* (78%) and *Australopithecus* LP (51%) (Table 8). On the LD1 versus LD2 plot, this specimen is just outside the comparative specimen polygons of *Australopithecus* LP and *Homo* EEA along the LD2 axis, giving it a more *Au. anamensis*-like LD2 score (Fig. 18). We assign this specimen to *Australopithecus* LP/*Homo* EEA (Table 2).

OMO 224-10005 is a right M₂ with moderate wear but no dentine exposure. This tooth shows an interrupted middle and distal trigonid crest, the Y-groove pattern, and a pronounced linear anterior fovea. There is a large hypoconulid and a moderately-sized C6. On the buccal surface, there is a slight protoconid groove. The linear dimensions all plot within the first stdv of *Australopithecus* LP and between the distributions of the larger *Homo* EEA and the smaller *H. erectus* (Fig. 7). The shape index also overlaps with *Australopithecus* LP, *Homo* EEA, *H. erectus*, and *P. boisei* (Fig. 7D). The LDA predictions are *Homo* (52%) and *Australopithecus* LP (50%) (Table 8). On the LDA graph, this tooth plots within a dense cluster of

comparative specimens from *Australopithecus* LP, *Au. anamensis*, *Au. deyiremeda*, *Homo* EEA, and *H. erectus* (Fig. 17). We assign this tooth to the *Australopithecus* LP/*Homo* EEA category (Table 2).

OMO 329-10015 is a small mandibular M₃ germ with linear dimensions that overlap with the smallest specimens of *Australopithecus* LP and *Homo* EEA, and close to or within the first stdv of *H. erectus* and *Ar. ramidus* (Fig. 8A-C). The shape index is in the overlapping range of all the comparative taxa with multiple specimens (Fig. 8D). The LDA predictions are *Homo* (66%) and *H. erectus* (47%) (Table 8). However, the plot on the LD1 versus LD2 graph places this specimen well within the *Australopithecus* LP polygon, in the overlap with *Homo* EEA and *H. erectus* (Fig. 18). The crown has a pronounced anterior fovea, a large hypoconulid, and a strong protostylid that extends mesially from the buccal groove. We designate this specimen as *Australopithecus* LP/*Homo* EEA (Table 2).

OMO 349-10003 is a worn lower left M₂ with dentine exposures on all buccal cusps. The morphology exhibits the Y-groove pattern, a slight anterior fovea, and a large hypoconulid equal in size to the entoconid. The linear dimensions plot below the first stdv of *Australopithecus* LP, below the range of variation typically seen for *Homo* EEA, and within the first stdv of *Ar. ramidus* and *H. erectus* (Fig. 7). The shape index plots within the first stdv of *Ar. ramidus*, *Australopithecus* LP, *H. erectus*, and *P. boisei*. The LDA predictions are *Homo* (56%) and *H. erectus* (51%) (Table 8). On the LD1 versus LD2 plot, OMO 349-10003 plots within a cluster of comparative specimens from *Ar. ramidus*, *Australopithecus* LP, *Au. anamensis*, and *H. erectus* (Fig. 17). Considering the mixture of taxonomic signals from the morphology and linear dimensions, we place this specimen within the *Australopithecus* LP/*Homo* EEA category (Table 2).

Member D (2.53 Ma to 2.39 Ma)

Two of the four specimens from Member D belong to the *Australopithecus* LP *Homo* EEA group and two are assigned to *Paranthropus* (Table 2).

L 9-12 is an upper left M³ (Howell & Coppens 1974) with relatively large linear dimensions that plot among the largest specimens attributed to *Australopithecus* LP and *Homo* EEA, and with the smallest specimens of *P. boisei* (Fig. 13). The shape ratio overlaps with all multi-specimen taxa except for *Ar. ramidus* (Fig. 13D). On the LD1 versus LD2 plot, L 9-12 plots at exactly the point where the *Australopithecus* LP, *Homo* EEA, and *P. boisei* polygons intersect (Fig. 18). The LDA predictions are *Australopithecus* (73%) and *Australopithecus* LP (62%) (Table 8). Morphologically, the crown shows a faint metacone, a large hypocone, and a small metaconule. There are crenulations on the lingual surface and there is a large distal fovea. The crown has the bulging lingual shape, and the closed occlusal foveal morphology associated

with *Paranthropus*. The linear dimensions occupy the intermediate LDA space that *P. aethiopicus* often occupies between *Australopithecus* and *Paranthropus*, and the morphological features are *Paranthropus*-like. Therefore, we assign it to *Paranthropus* (Table 2).

L 50-2 is a left M² (originally identified as left M³ by Howell & Coppens 1974). This crown displays a very large metacone and hypocone, and a small but double metaconule. The *crista obliqua* is continuous and the Carabelli-like cusp is large. Overall, the shape has the bulging lingual aspect that is more characteristic of *Paranthropus*. The MD dimension plots among the larger specimens of *Australopithecus* LP and *Au. anamensis*, and within the first stdv of *Homo* EEA (Fig. 12A). In contrast, the BL dimension plots within the first stdv of *Australopithecus* LP and *Au. anamensis* and among the larger specimens of *Homo* EEA and *H. erectus* (Fig. 12B). The shape ratio is at the higher end of the variation observed for *Australopithecus* LP, *Au. anamensis*, *Homo* EEA, *H. erectus*, and *P. boisei*, but closer to the first stdv of *Homo* EEA and *P. boisei* (Fig. 12D). The LDA predictions are *Homo* (61%) and *Homo* EEA (49%) (Table 8). On the LDA graph, L 50-2 plots in the overlap of *Australopithecus* LP and *Homo* EEA (Fig. 17). We weigh the morphology of this crown more heavily than the linear dimensions, as the *Paranthropus*-like characteristics are more pronounced than those of OMO 18-1970-1799, which is assigned to *Paranthropus*. Therefore, we assign L 50-2 to *Paranthropus* (Table 2).

L 441-10001 is an upper left P³. The linear size dimensions all plot in the overlap of *Australopithecus* and *Homo*, with the MDxBL dimension plotting on the mean for *Homo* EEA and very close to the mean of *Australopithecus* LP (Fig. 9, Supplemental Table S4). The shape index only overlaps with the variation observed for *Homo* EEA and *P. boisei* (Fig. 9D). When plotted along LD1 and LD2, L 441-10001 is just at the edge of the *Homo* EEA polygon, and close to the center of the *Au. anamensis* polygon, near the cluster of other *Australopithecus* species (Fig. 14). L 441-10001 is heavily crenulated and has mesial and distal accessory ridges, a pronounced transverse crest, and an equal bifurcation of the essential crests on both buccal and lingual cusps. The very oval/rounded shape of the crown is more aligned with *Homo* than *Australopithecus*. The hierarchical analysis of the morphological scores places this tooth within a cluster containing all *Australopithecus* LP/*Homo* EEA specimens (i.e., B 8-4Q and W 8-988; Fig. 19). The LDA predictions are *Homo* (61%) and *Homo* EEA (49%) (Table 8). We assign this tooth to *Australopithecus* LP/*Homo* EEA (Table 2).

L 824-5 is a lower left M₁ (Suwa *et al.* 1996). This fairly worn crown has dentine exposed on all buccal cusps, including the hypoconulid. This tooth was not included in the morphological score clustering analysis because it did not have all external features available. The linear dimensions are small, plotting among the smaller specimens attributed to *Australopithecus* LP and *H. erectus* for MD (Fig. 6A). The BL

dimension is on the smaller end of the range of variation but within the first stdv of *Homo* EEA and *H. erectus* (Fig. 6B). The size ratio is within the first stdv of *Australopithecus* LP and *H. erectus*, but also overlaps with *Ar. ramidus*, *Au. anamensis*, and *P. boisei* (Fig. 6D). Suwa *et al.* (1996) designated this crown as *Australopithecus/Homo* gen. and sp. indet. The LDA predictions are *Australopithecus* (64%) and *H. erectus* (47%) (Table 8). When plotted on the LD1 and LD2 axes, we see that the dimensions of L 824-5 plot in the overlap of the *Australopithecus* LP and *H. erectus* polygons (Fig. 16). We assign this tooth to *Australopithecus* LP/*Homo* EEA (Table 2).

Member E (2.39 Ma to 2.33 Ma)

Including the two specimens in the comparative dataset that represent *P. aethiopicus*, there are eight specimens from Member E. Four are assigned to *Paranthropus*, three are assigned to *Australopithecus* LP/*Homo* EEA, and one is assigned to *Australopithecus* LP (Table 2). Two of the *Au. afarensis/Homo* specimens have some affinity to *Paranthropus* but the weight of the evidence aligns them with *Australopithecus* LP/*Homo* EEA.

L 26-1g is a lower right M₁ (in agreement with the designation of Suwa 1996, and Suwa *et al.* 1996; identified as a right M₂ by Howell & Coppens 1974). The linear dimensions plot among the larger comparative specimens of *Australopithecus* LP and the smaller specimens of *P. boisei*, with no overlap in MD or MDxBL dimensions with other taxa (Fig. 6A, C). The shape index plots within the first stdv of *Homo* EEA (Fig. 6D). The LDA predictions are *Homo* (66%) and *Homo* EEA (79%) (Table 8). The LD1 and LD2 plot places L 26-1g just outside the *Paranthropus*, *Australopithecus* LP, and *Homo* EEA polygons (Fig. 18). Morphologically, this tooth presents the Y-groove pattern, a pronounced anterior fovea, a discontinuous middle trigonid crest, a hypoconulid larger than the entoconid, an equal-sized metaconid and hypoconid, and a smaller protoconid. We assign this tooth to *Australopithecus* LP/*Homo* EEA but note that the size of the entoconid is suggestive of *Paranthropus* (Table 2).

L 338/X-34 is an upper left M² (Howell & Coppens 1974). Morphologically, the tooth has a large metacone, a hypocone much larger than the metacone, and a small metaconule. It is worn very flat, a characteristic common in *Paranthropus*. Despite the wear, we see that it presents a continuous oblique and transverse crest and a small distal fovea. There is a large caries in the occlusal surface of the protocone. This is a large tooth that plots in the range of *P. boisei* for all size dimensions (Fig. 12A-C). The shape ratio is one of the highest in the comparative sample, only matched by two specimens in *Homo* EEA (KNM-ER 62000 and KNM-ER 1805) and one in *H. erectus* (KNM-WT 15000) (Fig. 12D). The LDA predictions are *Paranthropus* (100%) and *P. boisei* (100%) (Table 8). In the plot of LD1 and LD2 (Fig. 17), this specimen

extends the range of variation observed for *P. boisei*, but plots in a region of the graph that is difficult to interpret as anything other than *Paranthropus* (Table 2).

L 338/X-35 is a very large right P³ (Howell & Coppens 1974, identify this as a right P⁴) with no comparative specimen that matches its size. The MD and MDxBL values are beyond the range of the observed values in the comparative sample (Fig. 9A, C). The BL dimension plots within the range of variation observed for *P. boisei*, and is just below that of *Au. garhi* (Fig. 9B). The crown has the bulbous appearance characteristic of *Paranthropus*, with a continuous transverse crest, a distobuccal cusplet with a free apex and the bifurcation of buccal and lingual essential crests. The LDA predictions are *Paranthropus* (100%) and *Au. garhi* (100%) (Table 8). The LDA plot shows that this specimen is beyond the most extreme *P. boisei* specimens in our comparative sample (Fig. 14). This specimen is assigned to *P. boisei* (Table 2).

L 338/X-39 is a left M₃. We include this specimen in our comparative sample as *P. aethiopicus* based on the identification and description of Suwa *et al.* (1996).

L 338/X-40 is a left P₄. We include this specimen in our comparative sample as *P. aethiopicus* based on the identification and description of Suwa *et al.* (1996).

OMO 57/3-10010 is a lower right M₂. Its linear dimensions plot in the overlap of the first stdv of *Australopithecus* LP and *Homo* EEA (Fig. 7A-C). The shape ratio plots in the overlap of *Australopithecus* LP, *Homo* EEA, *H. erectus*, *P. boisei*, and the lowest values of *P. aethiopicus* (Fig. 7D). The LDA predictions are *Australopithecus* (51%) and *Australopithecus* LP (51%) (Table 8). On the LDA plot, this specimen's LD1 value is 0.45 and LD2 is 1.1. Because of how close the Omo specimens cluster in Fig. 17, this specimen is unlabeled. It plots in a cluster with L 7-279, L 1/nn-10010 a and b, and OMO K 7-1969-19. This region is within the overlap between the *Australopithecus* LP, *Homo* EEA, and *H. erectus* polygons (Fig. 17). Morphologically, this tooth exhibits a Y-groove pattern, a medium-sized hypoconulid, and an entoconulid with an enamel wrinkle. We assign it to *Australopithecus* LP/*Homo* EEA (Table 2).

OMO 166-1973-781 is a relatively large left M³ with linear dimensions that, like OMO 163-10001 and L 9-12, plot among the larger specimens of *Australopithecus* LP and *Homo* EEA, and the smaller specimens of *P. boisei* (Fig. 13A-C). The shape index is among the higher values observed for *Australopithecus* LP, *Homo* EEA, and *P. boisei* (Fig. 13D). The LDA predictions are *Australopithecus* (80%) and *Australopithecus* LP (66%) (Table 8). When plotted on the LD1 and LD2 axes, this specimen is very close to L 9-12, within the overlap of the *Australopithecus* LP and *Homo* EEA polygons, and very close to the edge of the *P. boisei* polygon (Fig. 18). Morphologically, this tooth has a large metacone and hypocone, a small metaconule and a continuous transverse crest. The crown is heavily worn but has no dentine exposed, and the

mesiobuccal cusp is higher than the others. We assign this tooth to *Australopithecus* LP/*Homo* EEA, but note that it potentially has affinities to *Paranthropus* (Table 2).

OMO 177-1973-4525 is a right P_3 (Suwa *et al.* 1996). This asymmetrical crown has a weakly developed lingual relative to buccal cusp. It also shows a distal accessory ridge and a pronounced transverse crest. The relatively small talonid and large protoconid differentiate this crown from *Paranthropus* (see Fig. 1 in Suwa *et al.* 1996), aligning the specimen with the non-robust taxa. The linear dimensions of this tooth are within the first stdv of *Homo* EEA and *P. aethiopicus* for MD, also overlapping with the larger *Australopithecus* LP and smaller *P. boisei* specimens (Fig. 4A). For the BL and MDxBL dimensions, OMO 177-1973-4525 is at the lower end of the variation observed for *P. boisei* and *P. aethiopicus*, and at the higher end of the variation observed for *Australopithecus* LP (Fig. 4B,C). The shape ratio plots within the overlap of all multi-specimen taxa (Fig. 4D). The LDA predictions are *Australopithecus* (61%) and *Australopithecus* LP (59%) (Table 8). On the LDA plot, this specimen is at the edge of the *Australopithecus* LP polygon, in the region between *Australopithecus* LP and *Paranthropus* (Fig. 14). Suwa *et al.* (1996) conclude that this specimen has similarities to *Homo*. None of our methodologies reveal a particular affinity to *Homo* compared to other taxa, and therefore we assign it to *Australopithecus* LP (Table 2).

Member F (2.32 Ma to 2.29 Ma)

There are twenty specimens from this Member, including the six included in our comparative dataset as *P. aethiopicus*. Of the others, six are assigned to *Australopithecus* LP/*Homo* EEA, six to *Homo* (or cf. *Homo*), one to cf. *Au. garhi*, and one to *Paranthropus* (Table 2). Given that we followed previous taxonomic designations for *P. aethiopicus*, it is possible that isolated postcanine teeth are easily intermixed between *P. aethiopicus* and *Au. garhi*, and therefore our tentative identification of the latter is incorrect, or vice versa.

F 22-1 includes a right M_2 and M_3 . We include this specimen in our comparative sample as *P. aethiopicus* based on the identification and description of Suwa *et al.* (1996).

L 28-30 is a right M_3 (Howell & Coppens 1974). L 28-30 is an unworn, heavily crenulated tooth with a discontinuous middle and distal trigonid crest. A thick and uninterrupted mesial marginal ridge encloses a pronounced anterior fovea. There is an L-shaped deflecting wrinkle and a cruciform groove pattern. The hypoconulid is large, almost the same size as the hypoconid, the entoconid is about half the size of the hypoconid, and the entoconulid is moderate in size. The MD dimension plots with the largest values of *Australopithecus* LP, *Au. anamensis*, and *Homo* EEA, and the smaller values of *P. boisei* (Fig. 8A). The BL dimension overlaps with values observed for *Ar. ramidus*, *Australopithecus* LP, *Au. anamensis*, *Homo* EEA,

H. erectus, and the smallest value attributed to *P. boisei* (KNM-ER 1480) (Fig. 8B). The MDxBL value plots within the values observed for *Australopithecus* LP, *Au. anamensis*, *Au. deyiremeda*, *Homo* EEA, and *P. boisei* (Fig. 8C). The shape index is unusual, in that it is larger than any of our comparative specimens, most similar to the largest values observed for *P. aethiopicus* and *Homo* EEA (Fig. 8D). The LDA predictions are *Australopithecus* (81%) and *Homo* EEA (54%) (Table 8). On the LDA graph, L 28-30 is outside the polygons of our comparative taxa (Fig. 18). For LD1, this specimen overlaps with the values attributed to *Paranthropus*, *Australopithecus*, and *Homo* EEA (Fig. 18). Along LD2, L 28-30 is most like *Homo* EEA on the species graph and *Paranthropus* on the genus graph, but close to *Homo* (Fig. 18). Suwa *et al.* (1996) classified this tooth as an indeterminate species of *Homo*. We assign L 28-30 to cf. *Homo* (Table 2).

L 28-58 is a right M¹ worn flat with dentine exposure on the lingual cusps and a likely caries on the mesiolingual cusp (Howell & Coppens 1974, identified this as a worn M²). The MD dimension of this crown plots alongside the largest measurements for *Homo* EEA and the smaller specimens of *P. boisei* (Fig. 11A). For the BL and MDxBL dimensions, L 28-58 is among the larger specimens of *Australopithecus* LP and *Homo* EEA (Fig. 11B,C). The shape index is high, being most similar to the range of values observed for *Homo* EEA and larger values of *H. erectus* and *Australopithecus* LP (Fig. 11D). The LDA predictions are *Homo* (76%) and *Homo* EEA (61%) (Table 8). On the LDA graph, L 28-58 plots just outside the *Australopithecus* LP and *Homo* EEA ranges, close to OMO 84-10001 (Member C or F, cf. *Homo*, Table 2) (Fig. 16). We assign this specimen to *Homo* (Table 2).

L 157-35 is a left M₂. We include this specimen in our comparative sample as *P. aethiopicus* based on the identification and description of Suwa *et al.* (1996).

L 238-35 is a right M² (Howell & Coppens 1974). This crown is worn flat (somewhat like *Paranthropus*) but with a small dentine exposure on the protone. L 238-35 has a large metacone and hypocone, a medium-sized metaconule and a continuous *crista obliqua*. The MD dimension is intermediate, plotting within the first stdv of *Australopithecus* LP, *Au. anamensis*, and *Homo* EEA (Fig. 12A). The BL dimension is comparatively larger, plotting alongside the largest specimens of *Au. anamensis* and *Homo* EEA, and the smallest specimen of *P. boisei*, with no overlap with the range of variation observed for other taxa (Fig. 12B). In its MDxBL dimension, L 238-35 is among the largest specimens of *Australopithecus* LP, *Au. anamensis*, and *Homo* EEA (Fig. 12C). The shape index is among the lowest observed in our comparative sample, near the lowest, outlier values for *H. erectus* (Sh.y.009 from China), *Australopithecus* LP (MSD-VP-1/53, a heavily eroded crown for which the MD and BL dimensions may be skewed), *P. boisei* (OH 5, which also has a broken M² with suspect linear dimensions), and *Ar. ramidus* (with multiple specimens at this low shape index). L 238-35's shape index is quite similar to the one value we know for *Au. garhi*, a

crown that is complete and undamaged (Fig. 12D). The LDA predictions are *Australopithecus* (71%) and *Australopithecus* LP (36%) (Table 8). On the LDA graph, this specimen is just outside the polygons for *Australopithecus* LP and *Au. anamensis*, plotting in the general area of the one specimen known for *Au. garhi* (Fig. 17). Given the unusualness of the shape index for *Au. garhi*, combined with the large size, and that M² is the most distinctive of the *Au. garhi* postcanine teeth when considered in isolation, we assign this specimen cf. *Au. garhi* (Table 2).

L 398-120 is a right P₃. We include this specimen in our comparative sample as *P. aethiopicus* based on the identification and description of Suwa *et al.* (1996).

L 398-573 is a left M³ (Howell & Coppens 1974). The MD dimension plots within the first stdv of *Australopithecus* LP and within the upper ranges of variation of *Homo* EEA and *H. erectus* (Fig. 13A). The BL dimension plots among the largest specimens of *Australopithecus* LP, *Homo* EEA, and within the first stdv of *P. boisei* (Fig. 13B). Overall size (MDxBL) is among the larger specimens of *Australopithecus* LP and *Homo* EEA (Fig. 13C). The size index is low, overlapping with the values observed for *H. erectus* and *Au. anamensis*, and to a lesser degree, *Ar. ramidus* and *P. boisei* (Fig. 13D). The LDA predictions are *Australopithecus* (66%) and *Australopithecus* LP (47%) (Table 8). On the LDA graph, this tooth plots within the polygons of *Homo* EEA and *Australopithecus* LP, very close to two specimens we attribute to *Australopithecus* LP/*Homo* EEA: L 220-10001 (Member C) and OMO 33-1970-63 (Member F), (Fig. 18). The crown displays a small metacone and hypocone, a small cuspule as a metaconule, and a continuous *crista obliqua*. We assign this specimen to *Australopithecus* LP/*Homo* EEA (Table 2).

L 398-630 is a right M₃ with the mesiolingual cusp broken. Only the MD dimension could be measured accurately, and this dimension plots alongside the largest dimensions observed for *Australopithecus* LP and *Homo* EEA, and among the smaller values of *P. boisei* (Fig. 8A). While the dimensions of L 398-630 are a little smaller than L 628-3 from Member G-3, morphologically the two crowns are similar in having relatively smaller lingual cusps compared to the buccal cusps that align them both with *Paranthropus* (character 3, Table 6), the “puffy” higher crown. Therefore, we assign this crown to *Paranthropus* (Table 2).

L 398-2608 is a right M³. The MD dimension plots within the first stdv of *Australopithecus* LP, *Au. anamensis*, and *Homo* EEA (Fig. 13A). The BL dimension is among the largest specimens of *Australopithecus* LP and the smallest specimen of *P. boisei* (Fig. 13B). The MDxBL dimension is therefore at the larger end of the range of variation of *Australopithecus* LP, *Au. anamensis*, *Homo* EEA, and alongside the largest specimen of *H. erectus* in our comparative sample (Fig. 13C). The shape ratio is low, plotting within the first stdv of *H. erectus*, and overlapping with the lowest values observed for *Ar. ramidus* and *P.*

boisei (Fig. 13D). The LDA predictions are *Australopithecus* (53%) and *Homo* EEA (32%) (Table 8). On the LDA graph, this tooth plots within the polygons of *Homo* EEA, *Au. anamensis*, and *Australopithecus* LP (Fig. 18). Morphologically, this specimen presents a small metacone and hypocone, a double medium-sized metaconule, a large distal fovea and some mesial marginal tubercles. Combining all these lines of evidence, we assign this tooth to *Australopithecus* LP/*Homo* EEA (Table 2).

L 860-2 is a mandible with a right P₃ and M₂, and a left P₃ and P₄. We include this specimen in our comparative sample as *P. aethiopicus* based on the identification and description of Suwa *et al.* (1996).

OMO 33-1969-9 is a right M₃. We include this specimen in our comparative sample as *P. aethiopicus* based on the identification and description of Suwa *et al.* (1996).

OMO 33-1970-63 is a right M³ (Howell & Coppens 1974, identified this as either an M¹ or M²). Morphologically, OMO 33-1970-63 has a weak metacone, a large hypocone and a medium-sized metaconule. The linear dimensions show that this is a large tooth, plotting among the larger specimens of *Australopithecus* LP and *Homo* EEA (Fig. 13A-C). The shape ratio is also large, plotting within the first stdv of *P. boisei*, and within the larger values observed in *Australopithecus* LP and *Homo* EEA (Fig. 13D). The LDA predictions are *Australopithecus* (76%) and *Australopithecus* LP (60%) (Table 8). On the LDA graph, this specimen plots in a tight cluster with L 398-573 (Member F, *Australopithecus* LP/*Homo* EEA, Table 2) and L 220-10001 (Member C, *Australopithecus* LP/*Homo* EEA, Table 2), within the polygons of *Australopithecus* LP and *Homo* EEA (Fig. 18). We therefore assign this specimen similarly to *Australopithecus* LP/*Homo* EEA (Table 2).

OMO 33-1971-506 is a right P³ (Howell & Coppens 1974). The linear dimensions of this crown show a closer affinity to *Au. anamensis*, and to a lesser degree *Homo* EEA and *Australopithecus* LP (Fig. 9A-C). The shape ratio overlaps with all multi-specimen taxa except for *Ar. ramidus* (Fig. 9D). The LDA predictions are *Australopithecus* (55%) and *Australopithecus* LP (37%) (Table 8). On the LDA graph, this tooth plots in a dense cluster of comparative specimens that belong to *Australopithecus* LP, *Homo* EEA, and *Au. anamensis* (Fig. 14). Morphologically, the crown is worn flat (like *Paranthropus*), with cusps approximately equal in size. We assign this crown to *Australopithecus* LP/*Homo* EEA (Table 2).

OMO 33-508 is a right P₄. We include this specimen in our comparative sample as *P. aethiopicus* based on the identification and description of Suwa *et al.* (1996).

OMO 33-1973-3282 is a left P⁴. The specimen is worn flat, similar to what is characteristic of *Paranthropus*. Despite the wear, we can discern that it has a distal accessory ridge, a discontinuous transverse crest and a marked groove on the distobuccal surface but with no projection. It exhibits a single buccal essential crest and a bifurcated lingual one. The linear dimensions are relatively small, overlapping

most with *Ar. ramidus* and the two *Homo* categories (Fig. 10A-C). The shape ratio is intermediate, overlapping with all of the comparative taxa save for *Ar. ramidus* (Fig. 10D). The LDA predictions are *Homo* (61%) and *H. erectus* (44%) (Table 8). On the LDA graph, the LD1 and LD2 values plot within a dense cluster of comparative specimens categorized as *H. erectus*, *Australopithecus* LP, and *Au. deyiremeda*, and close to OMO 69-1974-900 (Member C, *Australopithecus* LP/*Homo* EEA) and B 8-23A (Member B, *Australopithecus* LP) (Fig. 15). We assign this specimen to the *Australopithecus* LP/*Homo* EEA category (Table 2).

OMO 33-1973-5496 is a left P_3 (Suwa *et al.* 1996). The MD dimension plots within the first stdv of *Australopithecus* LP and *Homo* EEAA, overlapping the larger values within *H. erectus* and the lower values within *P. aethiopicus* (Fig. 4A). The BL dimension overlaps with the larger *Australopithecus* LP and the smallest *P. boisei* (Fig. 4, Pane B). The MDxBL value is within or very close to the first stdv of *Australopithecus* LP and *Homo* EEA, without overlapping other comparative taxa (Fig. 4C). The size ratio overlaps with all multi-specimen comparative taxa (i.e., all but *Au. deyiremeda*). The LDA predictions are *Australopithecus* (65%) and *Australopithecus* LP (64%) (Table 8). When plotted on the LDA graph, OMO 33-1973-5496 plots well within the *Australopithecus* LP polygon, close to the overlap with the *Homo* EEA polygon (Fig. 14). This is a heavily worn crown with dentine exposure on the buccal cusp. It has distal and mesial grooves on the buccal surface. Suwa *et al.* (1996) concluded that this specimen has affinities to *Homo* whereas Schwartz and Tattersall (2003) considered this specimen to belong to the *Paranthropus* lineage. We assign this specimen to *Australopithecus* LP/*Homo* EEA (Table 2).

OMO 123/N-1973-5495 is a right P_3 (Suwa *et al.* 1996). While the tooth is worn, it is not flat like is characteristic of *Paranthropus*. It displays a pronounced transverse crest, a groove on the distobuccal and mesiolingual surfaces and three lingual cusps. The crown is asymmetrical with a mesial placement of the metaconid relative to the protoconid. The linear dimensions are among the larger values observed in *Australopithecus* LP and the lower values of *P. boisei*, overlapping *Homo* EEA in MD length (Fig. 4). The shape index is most similar to *Australopithecus* LP, *H. erectus*, and *P. boisei* (Fig. 4D). The LDA predictions are *Australopithecus* (61%) and *Australopithecus* LP (62%) (Table 8). On the LDA graph, this specimen plots in the center of the comparative specimens, in between the *P. boisei* and *Australopithecus* LP polygons, but not within either of them (Fig. 14). These LD1 and LD2 values cluster with two other Omo specimens: OMO 29/1-1968-43 (cf. *Homo*) and OMO 75-1969-14b (*Homo*), both from Member G (Fig. 14). Suwa *et al.* (1996) concluded that this specimen has affinities to *Homo*. In agreement with Suwa *et al.* (1996), we also assign this specimen to cf. *Homo* (Table 2).

OMO 174-10002 is a left M₃. The linear dimensions of this tooth and the shape ratio plot within the variation of *H. erectus* and *Ar. ramidus* with only minimal overlap with other taxa (Fig. 8). The LDA predictions are *Homo* (67%) and *H. erectus* (52%) (Table 8), and in the LDA graph this tooth is within the *H. erectus* polygon with overlap to one end of the *Australopithecus* LP polygon (Fig. 18). The morphology supports a *Homo* classification as the crown exhibits a large hypoconulid and a medium-sized metaconulid. There is a Y-groove pattern and a pit in the groove of the buccal surface. We assign this specimen to *Homo* (Table 2).

OMO 371-10035 is a small left M₃. It is smaller than all of our comparative specimens, plotting near the lowest point on the y-axis for all three size dimensions in Fig. 8A-C. The LDA predictions are *Ardipithecus* (94%) and *Ar. ramidus* (86%) (Table 8). However, the morphology of this specimen is *Homo*-like in that the distal half of the crown is reduced in size, with a relatively small entoconid and hypoconid. The crown also has a cruciform-groove pattern. This affinity to *Homo* is also evident in the LDA graph, as this specimen plots at the lowest values of LD1, just past the polygon of *H. erectus* (Fig. 18). We assign OMO 371-10035 to *Homo* (Table 2).

P 933-1 is an unworn left M¹ (Howell & Coppens 1974) with linear dimensions that plot in the upper ranges of *Australopithecus* LP, *Homo* EEA, and *H. erectus* (Fig. 11A-C). The shape ratio is more similar to *Homo* EEA and *H. erectus*, but overlaps with the largest values observed in *Australopithecus* LP and the highest value for *P. boisei* (Fig. 11D). The LDA predictions are *Homo* (82%) and *Homo* EEA (60%) (Table 8). On the LDA graph, P 933-1 plots in the overlap of the *Australopithecus* LP and *Homo* EEA polygons, and just at the edge of the *H. erectus* polygon (Fig. 16). We assign this specimen to *Homo* (Table 2).

Member G (2.27 Ma to 1.91 Ma)

There are 23 specimens in Member G. Thirteen are assigned to *Paranthropus*, *P. boisei*, or with affinities to *Paranthropus*. Eight are classified as *Homo* or with affinities to *Homo*. One specimen is attributed to *Australopithecus* LP/*Homo* EEA, and another can only be assigned to hominin (Table 2).

L 7-279 is a left M₂ (Howell & Coppens 1974; Suwa *et al.* 1996). The clustering analysis was not possible for this tooth because it did not have all external features observable. The linear dimensions and shape ratio plot close to those of OMO 57/3-10001 and L 1-398 (Fig. 7A-C), both assigned to *Australopithecus* LP/*Homo*EEA (Table 2). The LDA predictions are *Australopithecus* (56%) and *Australopithecus* LP (51%) (Table 8). On the LDA graph, L 7-279 plots in a dense cluster of comparative specimens representing *Australopithecus* LP and *Homo* EEA (Fig. 17). The crown is fairly worn in the asymmetrical pattern associated with the non-robust hominins. Most notably, there is a large caries that encompasses most of

the occlusal surface of the protoconid. Suwa *et al.* (1996) concluded that this crown has affinity to *Homo* sp. indet. Given the exclusive overlap with the *Homo* polygons on the LDA graph, and the non-robust morphology, we assign this tooth to *Homo* (Table 2).

L 7/A-125 is a nearly complete mandible with heavily worn dentition. This specimen is often variously-labeled in the literature as L7a-125 or L7-125. The most complete crowns are a left M₃, left P₄, and right M₃ (Howell 1969; Howell & Coppens 1974). This is a heavily robust specimen with large postcanine teeth and very small anterior dentition. The specimen is widely recognized as *P. boisei* (Howell 1969; Suwa *et al.* 1996; Grine *et al.* 2019). Our analyses concur, with the LDA predictions for the M₃ being *Paranthropus* (83% and 82%) and *P. boisei* (98% and 89%) (Table 8). And, the LDA predictions for the P₄ are *Paranthropus* (100%) and *P. boisei* (100%) (Table 8). Interestingly, the P₄ plots within the *Paranthropus* genus polygon but outside both *Paranthropus* species polygons (Fig. 15). Similarly, the M₃s also plot outside but near the *Paranthropus* polygons (Fig. 18). Accordingly, we assign this specimen to *P. boisei* (Table 2).

L 74/A-21 is a right hemi-mandible with associated maxillary and mandibular dental remains (Howell & Coppens 1974). This specimen is sometimes labeled as L 74A-21, L 74a-21, or L74-21 in the literature. We only include the well-preserved right P₄ in our analysis. This molariform P₄ exhibits a disto-buccal cusplet with a free apex and three lingual cusps. The metaconid is placed in a mesial position, the transverse crest is interrupted by the sagittal fissure, and there is a deep distal fovea. The crown has a substantial talonid, and the cusp tips are mesially oriented, like *Paranthropus*. Suwa *et al.* (1996) similarly assigned this specimen to *Au. aff. boisei* based on their analysis of the crown morphology of the P₄. Howell (1969) noted the extreme robusticity of the mandible and tooth crowns, interpreting this to be from a robust species of *Australopithecus* (what would now commonly be referred to as *Paranthropus*). Grine *et al.* (2019) also assigned this specimen to *P. boisei*. The LDA predictions are *Paranthropus* (87%) and *P. boisei* (77%) (Table 8). On the LDA graph, this P₄ plots within the *P. boisei* polygon, but is close to the overlap with the *Australopithecus* LP polygon (Fig. 15). The linear dimensions are most similar to those of *P. boisei* (Fig. 5). We assign this specimen to *Paranthropus* (Table 2).

L 427-7 is a partial right mandible with erupting P₃ (A), P₄ in crypt (B), roots of dm₂ and M₁, and a complete M₂ (C) (Howell & Coppens 1974; Suwa *et al.* 1996). We do not discuss the mandibular morphology here as it is beyond the scope of this specific investigation. The right P₄ of L 427-7 is not included in the metric analysis, since not all dimensions could be measured. For the P₃, the linear dimensions plot consistently at the smaller end of the range of variation of *P. aethiopicus*, overlapping with the largest or smallest of the *Australopithecus* LP measurements depending on the parameter (Fig. 4A-C). The shape index is also most similar to *P. aethiopicus*, essentially overlapping with the mean for

that species (Fig. 4D). The LDA for the P_3 predicts *Australopithecus* (51%) and *P. aethiopicus* (65%) (Table 8). On the LDA graph, this P_3 plots in the *Australopithecus* LP polygon, beside the *P. aethiopicus* polygon (Fig. 14). The linear dimensions of the M_2 of L 427-7 plot with the larger specimens of *Homo* EEA, the largest of *Australopithecus* LP, and the smallest of *Paranthropus* (Fig. 7A-C). The shape index is close to the means of *P. boisei*, *H. erectus*, and *Australopithecus* LP (Fig. 7D). The LDA predictions for the M_2 are *Australopithecus* (58%) and *Homo* EEA (57%) (Table 8). Graphically, the LDA dimensions plot in the polygon of *Homo* EEA, in between the polygons of *Australopithecus* LP, *P. boisei*, and *P. aethiopicus* (Fig. 17). The morphology of all three crowns associate them most with *Paranthropus*. The right P_3 shows the mesially-positioned cusps and an extended talonid, as does the P_4 (although this is more difficult to discern as the specimen is obscured in part by the surrounding bone of the crypt). The right M_2 has a slight mesial fovea, discontinuous middle and distal trigonid crest and an L-shaped deflecting wrinkle. There is a medium hypoconulid and a moderate double entoconulid. The buccal cusps are more lingually positioned, giving the crown a more *Paranthropus*-like appearance (character 3, Table 6). A secondary groove extends across most of the buccal surface of the protoconid. This mandible was determined to have affinities to *P. boisei* in previous analyses (Suwa *et al.* 1996; Grine *et al.* 2019). We assign this specimen to *Paranthropus*, with the strongest evidence deriving from the P_3 (Table 2), noting that if the M_2 were discovered in isolation, we would have assigned it to *Australopithecus* LP/*Homo* EEA.

L 628-1 is a left P_4 (Suwa *et al.* 1996; originally identified as a left P^4 , Howell & Coppens 1974). This tooth is morphologically unusual because it has an odontoma in the middle of the occlusal surface. There is a mesial and distal accessory ridge and a disto-buccal cusplet with a free apex. There are more than three lingual cusps and the metaconid is in a medial position relative to the protoconid. The crown has the “puffy”, rounded appearance associated with *P. boisei*. The LDA predictions are *Paranthropus* (100%) and *P. boisei* (100%) (Table 8), which is not surprising given that the linear dimensions are all within the *P. boisei* range, only overlapping with the largest MD values observed in *Australopithecus* LP (Fig. 5). We assign this tooth to *Paranthropus* (Table 2).

L 628-2 is a mostly-complete right M_3 that has lost the enamel from the lingual side of the crown. However, the MD dimension can be estimated as 18.8 mm, clearly aligning this crown to *Paranthropus* in terms of size (Fig. 8A). Morphologically, L 628-2 has the rounded morphology and cusp proportions (e.g. character 3, Table 6) of *Paranthropus*, being very similar in appearance to L 157-35, one of the comparative specimens for *P. aethiopicus*. We assign this tooth to *Paranthropus* (Table 2).

L 628-3 is a left M_3 (Howell & Coppens 1974; Suwa *et al.* 1996). The linear dimensions of this tooth are very similar to, but just slightly larger than those of OMO 136-1972-1, assigned to *Paranthropus* (Table 2).

The LDA predictions are *Paranthropus* (61%) and *P. boisei* (59%) (Table 8). On the LDA graph, this tooth plots in the *Paranthropus* polygon, close to the *Australopithecus* LP overlap area (Fig. 18). This lower molar exhibits a large hypoconulid. The entoconulid and metaconulid are small compared to the buccal cusps, a reflection of character 3 (Table 6), used to differentiate *Paranthropus* from other hominins. Our conclusion on the taxonomic assignment of this crown accords with that of Suwa *et al.* (1996) and Grine *et al.* (2019). We assign this tooth to *Paranthropus* (Table 2).

L 628-4 is a left P_4 (Howell & Coppens 1974; Suwa *et al.* 1996). The asymmetrical morphology of the crown exhibits the mesially oriented cusps with an extended talonid and flat occlusal wear that are characteristic of *Paranthropus* (Suwa *et al.* 1996). This morphology combines with small linear size dimensions that align it more with the non-robust hominins in our comparative sample (Fig. 5A-C). The LDA predictions are *Australopithecus* (73%) and *Australopithecus* LP (56%) (Table 8). On the LDA graph, L 628-4 plots within the overlap of the *Australopithecus* LP, *Au. anamensis*, *Homo* EEA, and *H. erectus* polygons, but very close to the *P. aethiopicus* polygon (Fig. 15). The shape ratio of this crown is more similar to the means of *P. aethiopicus* and *H. erectus* than to other taxa (Fig. 5D), which is probably driving the *P. aethiopicus* similarity in the LDA. Suwa *et al.* (1996) concluded that this tooth has affinities to *P. aethiopicus* and *P. boisei*. Grine *et al.* (2019) also assigned this P_4 to *P. boisei*. We do not have evidence to support a confident assignment to *Paranthropus*, but do place more emphasis on the morphology than the size of the crown, and assign this tooth to cf. *Paranthropus* (Table 2). We note, however, that if this tooth is *Paranthropus*, it is slightly smaller than the smallest *P. aethiopicus* in our comparative dataset (OMO 18-1968-31, Member C) but has more strongly expressed *Paranthropus* morphological characteristics than OMO 18-1968-31.

L 628-9 is a left M_1 (Suwa 1996; Suwa *et al.* 1996; originally identified as a left M_2 , Howell & Coppens 1974). The linear dimensions of this crown plot most closely to the mean of *P. boisei*, but also overlap with the larger specimens of *Australopithecus* LP (Fig. 6A-C). The shape ratio is at the lower end of the observed values for *P. boisei*, plotting most closely to the means of *H. erectus*, *Australopithecus* LP, and *Ar. ramidus* (Fig. 6D). The LDA predictions are *Australopithecus* (67%) and *Australopithecus* LP (69%) (Table 8). On the LDA graph, L 628-9 plots close to a cluster of *Australopithecus* LP that is just on the edge of the *Paranthropus* polygon (Fig. 16). Morphologically, this molar presents a pronounced anterior fovea, a discontinuous middle trigonid crest and a deflecting L-shaped wrinkle. It has a medium-sized hypoconulid and a double and moderate entoconulid. Suwa *et al.* (1996) assigned this crown to *Paranthropus*, noting its similarities to *P. boisei*. Because the occlusal fovea is more lingually oriented (i.e., more closed,

character 3, Table 6), we agree with Suwa *et al.* (1996) and categorize this tooth as *Paranthropus* (Table 2).

L 628-10 is a left M₂ that is missing the enamel from the metaconid. Therefore, only the MD dimension could be measured. This dimension plots within the first stdv of *Australopithecus* LP and *Homo* EEA (Fig. 7A). Morphologically, this crown is very similar to the less-worn L 628-9, including evidence of a pronounced anterior fovea and large buccal cusps relative to the lingual cusps (character 3, Table 6). Because this specimen is from the same locality as L 628-9, shares so much of the same morphological features with L 628-9 and is just a little MD smaller, we assign L 628-10 to cf. *Paranthropus* (Table 2).

L 726-11 is a fragment of a right P⁴ missing the lingual half of the lingual cusp. The MD dimension can be estimated (12.2 mm), demonstrating one of the largest dimensions observed in our comparative samples, aligning with the largest dimensions observed for *Au. anamensis*, *Australopithecus* LP, and *P. boisei* (Fig. 10A). Morphologically, the occlusal fovea is crenulated and lacks the crest the typically connects the mesial and lingual cusps in *Australopithecus*. This feature aligns more with *Au. garhi*, *Homo* EEA, and *Paranthropus*. Therefore, we assign L 726-11 only to hominin, as we cannot differentiate the size and morphology more specifically between these three possible genera (Table 2).

L 894-1 is a partial maxillary dentition associated with craniofacial fragments that is interpreted as an early representative in the genus *Homo* (Boaz & Howell 1977; Kimbel 2009). We could reliably measure the linear dimensions for five teeth: right P³, right P⁴, right M¹, and right and left M³. All of the crowns are worn flat, though with no dentine exposure and some asymmetrical topography, slanting from the buccal cusps to the lingual cusps that are more worn. Given the high degree of wear, the morphology is difficult to discern. For the P³, the MD dimension plots within the first stdv of *Au. anamensis* and with larger values observed for *Homo* EEA (Fig. 9A). The BL and the MDxBL dimensions overlap with *Australopithecus* LP, *Au. anamensis*, *Homo* EEA, and *H. erectus* (Fig. 9B,C). The size index plots within the overlap of all the comparative taxa save for *Ardipithecus* (Fig. 9D). On the LDA graph, the P³ plots within a dense cluster of comparative specimens attributed to *Homo* EEA, *H. erectus*, *Australopithecus* LP, and *Au. anamensis* (Fig. 14). For the P⁴, the MD overlaps with the first stdv of *Australopithecus* LP, *Au. anamensis*, and *Homo* EEA (Fig. 10A). The BL dimension plots close to the means of *Australopithecus* LP, *Au. deyiremeda*, *H. erectus*, and *Homo* EEA (Fig. 10B). The MDxBL value is the most similar to *Au. deyiremeda* and *Homo* EEA (Fig. 10C). The shape index is most similar to *Australopithecus* LP, *Au. anamensis*, and *Homo* EEA (Fig. 10D). On the LDA graph, the LD1 and LD2 values for this P⁴ plot within a dense cluster of comparative specimens from *Homo* EEA and *Australopithecus* LP (Fig. 15). The linear dimensions of the M¹ plot in the area of overlap between *Australopithecus* LP, *Au. anamensis*, *Homo* EEA, and to a certain degree, *H. erectus* (Fig. 11A-C).

The shape index is more similar to *Australopithecus* LP, and *P. boisei* than to *Homo*, although it does overlap with the lower values of *H. erectus* (Fig. 11D). On the LDA graph, this tooth plots within a dense cluster of comparative data representing *Homo* EEA, *H. erectus*, *Australopithecus* LP, and *Au. anamensis* (Fig. 16). The linear dimensions and the shape index of the M³s, like the M¹ plot within the overlap of *Australopithecus* LP, *Au. anamensis*, *H. erectus*, and *Homo* EEA (Fig. 13A-D). On the LDA graph, both of the M³s plot together within a cluster of comparative specimens of *Homo* EEA, *Au. anamensis*, and *Australopithecus* LP (Fig. 18). The LDA predictions for all of these teeth are the same: *Australopithecus* for the genus (P³ = 48%; P⁴ = 49%; M¹ = 58%; and the M³s are both 54%; Table 8). The LDA predictions for species are all to *Australopithecus* LP (P³ = 38%; P⁴ = 50%; M¹ = 41%; and the M³s are both 37%; Table 8). However, the second most-likely prediction for genus reveals a close affinity to *Homo* (Supplemental Table S8), especially for the premolars, where the likelihoods are essentially the same for *Australopithecus* and *Homo* (48.0% versus 46.9% for the P³, and 48.9% versus 48.8% for the P⁴, respectively). The right P⁴ has an interproximal wear groove on the distal aspect (at the contact with the M¹) that has been interpreted as the earliest evidence of tooth-picking (Hlusko 2003). Using our method, these teeth are assigned to *Australopithecus* LP/*Homo* EEA (Table 2).

OMO Sh 1/1-1969-17 is a left M¹ (Howell & Coppens 1974). The linear dimensions of this crown plot within the first stdv of *Homo* EEA for MD, BL, MDxBL, and the shape ratio (Fig. 11). The morphology of this upper molar is characterized by a large metacone and hypocone and a continuous oblique crest. The LDA predictions are *Homo* (90%) and *Homo* EEA (74%) (Table 8), and on the LDA graph, it plots in the *Homo* EEA polygon, with slight overlap to the *H. erectus* polygon, and no overlap with the polygons of *Australopithecus* (Fig. 16). We assign this crown to *Homo* (Table 2).

OMO 29/1-1968-43 is a right P₃ (Howell & Coppens 1974; Suwa *et al.* 1996). The linear dimensions of this crown are very similar to those of OMO 75-1969-14 (Fig. 4A-C), only differing in having a lower shape ratio that overlaps with the first stdv of *Australopithecus* LP, *H. erectus*, and *P. boisei* (Fig. 4D). The LDA predictions are *Australopithecus* (60%) and *Australopithecus* LP (60%) (Table 8). On the LDA graph, OMO 29/1-1968-43 is right beside OMO 75-1969-14b, within the *P. boisei* polygon, and close to the *Australopithecus* LP polygon (Fig. 14). The asymmetric lower P₃ shows a distal accessory ridge, a pronounced transverse crest and a disto-buccal cusplet with a free apex. There are three lingual cusps and a medially positioned metaconid relative to the protoconid. The morphology is more aligned with the non-robust taxa as described by Suwa *et al.* (1996) in that the main cusps are not mesially positioned and the talonid is not expanded as seen in *Paranthropus*. Suwa *et al.* (1996) concluded that this specimen has

affinity to *Homo* sp. indet. Given the similarity to OMO 75-1969-14, and the morphology of the crown, but keeping in mind the results from our LDA, we classify this specimen as cf. *Homo* (Table 2).

OMO 47-1968-46 is a partial right M₂ missing the mesiobuccal aspect of the protoconid (Howell & Coppens 1974; Suwa *et al.* 1996). This crown is remarkably similar to OMO 47-1973-1500 in terms of both size, morphology, and wear. Suwa *et al.* (1996) concluded that this crown has affinities to *P. boisei*. We assign this tooth to *P. boisei* (Table 2).

OMO 47-1973-1500 is a right M₂ (Suwa *et al.* 1996). The linear dimensions of this tooth are very similar to those of OMO 75-1969-14, also from Member G and assigned to *Homo* (Table 2), but with MD and BL dimensions that overlap with *P. aethiopicus*, the largest specimens of *Australopithecus* LP and *Homo* EEA, and the smallest specimens of *P. boisei* (Fig. 7A-C). The shape ratio similarly overlaps with *Australopithecus* LP, *Homo* EEA, *H. erectus*, and both species of *Paranthropus* (Fig. 7D). The LDA predictions are *Australopithecus* (55%) and *Homo* EEA (51%) (Table 8). On the LDA plot, OMO 47-1973-1500 plots very close to OMO 75-1969-14h, within the *P. aethiopicus* polygon, just beside the *Homo* EEA polygon (Fig. 17). Morphologically, the entoconid is proportionately small, the hypoconulid is large, and the crown is worn very flat with no dentine exposure, features that are characteristic of *P. boisei*. Previous analyses similarly noted the affinity of this specimen to *P. boisei* (Suwa *et al.* 1996; Grine *et al.* 2019). We assign this tooth to *P. boisei* (Table 2).

OMO 75-1969-14 consists of partial maxillary and mandibular remains preserving nine teeth: left and right P₃, right P₄, right M₁, left and right M₂, left M₃, and in the maxilla there is the left P⁴ and the right M³ (Howell & Coppens 1974). This specimen provides the opportunity to compare how teeth from the same individual are classified in our analyses. We describe the teeth individually, and after, summarize the results and present our final taxonomic assignment.

The linear metrics of the left (OMO 75-1969-14b) and right (OMO 75-1969-14e) P₃s are in the larger size range, with MD dimensions in the first stdv of *P. boisei*, and overlapping with the largest specimens of *Australopithecus* LP, *Homo* EEA, and *P. aethiopicus* (Fig. 4A). The BL dimensions are within the larger dimensions of *Australopithecus* LP and the smallest of *P. boisei*, with no other overlap (Fig. 4B). The MDxBL size is within the first stdv of *P. aethiopicus*, the smallest values for *P. boisei*, and the largest values of *Australopithecus* LP, with no other taxonomic overlap save for one outlier, an unusually high value in *H. erectus* (D2600 from Dmanisi) (Fig. 4C). The shape index for the right P₃ is among the higher values observed for *Australopithecus* LP, *Homo* EEA, and *H. erectus*, while the shape index for the left P₃ is within the first stdv of *Australopithecus* LP, *H. erectus*, and *P. boisei* (Fig. 4D). LDA predicts *Australopithecus* (57% for both teeth) and *Australopithecus* LP (b = 59%, e = 55%) (Table 8). On the LDA graph, the left P₃ plots

within, but near the edge of the *P. boisei* polygon closest to *Australopithecus* LP (Fig. 14). The right P_3 plots outside of all comparative taxa polygons, but close to that of *P. boisei*, near *Australopithecus* LP and its overlap with *H. erectus* (Fig. 14). The linear metrics of the right P_4 plot with those of the largest *Australopithecus* and *P. aethiopicus* (Fig. 5A-C). The shape ratio has the greatest affinity to *Australopithecus* LP, *Homo* EEA, and *P. boisei* (Fig. 5D). LDA predictions are *Australopithecus* (81%) and *Australopithecus* LP (72%) (Table 8). On the LDA graph, this specimen plots within the *Australopithecus* LP polygon, close to the *Au. anamensis* and *Homo* EEA polygons, but without overlapping them (Fig. 15). Morphologically, these premolars do not have the mesially positioned cusps and extended talonid of *Paranthropus*, further bolstering an *Australopithecus* LP/*Homo* EEA designation.

The linear dimensions for the right M_1 all plot in the overlap between the largest *Australopithecus* LP and the smaller *P. boisei* (Fig. 6A-C). The shape ratio plots in the overlap between almost all of our comparative taxa except for *Ar. ramidus* (Fig. 6D). The LDA predictions are *Homo* (51%) and *P. aethiopicus* (53%) (Table 8). On the LDA graph, the specimen plots within the LD1 range of *Paranthropus*, but just above the polygon on the LD2 axis, outside of any of the comparative sample polygons (Fig. 16). The two closest specimens are L 26-1g (*Australopithecus* LP/*Homo* EEA with affinities to *Paranthropus*, Table 2) and L 628-9 (*Paranthropus*, Table 2). The linear dimensions of right (OMO 75-1969-14c) and left (OMO 75-1969-14h) M_2 s plot within the values observed for *P. aethiopicus*, the lower values for *P. boisei*, and the largest values of *Australopithecus* LP (Fig. 7A-C). The size ratios also plot within the first stdv of *P. aethiopicus*, as well as the higher values of *Australopithecus* LP, *Homo* EEA, *H. erectus*, and *P. boisei* (Fig. 7D). The LDA predictions at the genus level are *Australopithecus* (50%) and *Paranthropus* (53%) and at the species level, *P. aethiopicus* for both teeth (48% and 87%) (Table 8). The LDA graph shows both teeth plotting within the *P. aethiopicus* polygon, with the right M_2 being close to the *Homo* EEA polygon, but not within it (Fig. 17). Both M_2 s present a slight linear depression in the mesial marginal complex and discontinuous middle and distal trigonid crests. They have large hypoconulids and metaconulids and moderate entoconulids. The buccal surface of their protoconids exhibits a secondary groove that can be easily seen. Protostylid expression is at a state of 6. The MD, BL, and MDxBL values for the left M_3 plot within the first stdv of *Australopithecus* LP, *Au. anamensis*, and *Homo* EEA, overlapping with the largest specimens of *H. erectus* (Fig. 8A-C). The shape ratio is at the lower end of the comparative data, plotting within the first stdv of *Ar. ramidus* and *H. erectus*, and overlapping with the smaller values observed for *Australopithecus* LP, *Au. anamensis*, and *P. boisei* (Fig. 8D). The LDA predicts *Australopithecus* (68%) and *Australopithecus* LP (57%) (Table 8). On the LDA graph, this tooth plots within the dense cluster of comparative specimens assigned to *Australopithecus* LP, *Homo* EEA, and *Au. anamensis* (specimen not

labeled in Fig. 18; values are LD1 = -0.17; LD2 = 0.49). Morphologically, these molars have varying degrees of wear. Importantly, the wear is asymmetrical on the occlusal surface, a trait that is associated with non-robust hominins. Additionally, the position of the cusps is close to the crown margin, further aligning the morphology with *Australopithecus* and *Homo* rather than *Paranthropus* (character 3, Table 6). The left M₂ and M₃ have strong protostylids, with the M₂ expression being greater than that of the M₃, a trend associated with *Australopithecus* more than *Homo* (Husko 2004). Therefore, despite the strong association with *Paranthropus* in terms of linear dimensions, the morphological features of the crowns reject that taxonomic assignment.

The linear dimensions of the left P⁴ plot among the larger values observed for *Australopithecus* LP and below the smallest observed for *P. boisei* (Fig. 10A-C). The shape ratio plots within the first stdv of *Homo* EEA, but also overlaps with the highest values observed for *Au. anamensis*, *Australopithecus* LP, and *H. erectus* (Fig. 10D). The LDA predictions are *Australopithecus* (91%) and *Au. anamensis* (46%) (Table 8). On the LDA graph, this tooth plots within the *Australopithecus* LP polygon, close to both the *Au. anamensis* and the *Homo* EEA polygons, but not overlapping them (Fig. 15). The partial right M³ is not included in the LDA, as the buccolingual dimension could not be measured. However, the MD dimension is identical to *Au. garhi* (BOU-VP-12/130), and within the first stdv observed for *P. boisei* (Fig. 13A).

In summary, the analysis of the linear dimensions of the teeth of **OMO 75-1969-14** show a strong affinity to *Paranthropus*, and in particular, *P. aethiopicus*. This is an interesting result because it is at odds with previous taxonomic identifications of the specimen overall. Historically, this specimen has been assigned to both *Australopithecus* (Coppens 1980; Wood and Leakey 2011) and to *Homo* (Suwa *et al.* 1996; Grine *et al.* 2019; Schrenk *et al.* 2015). Unfortunately, Wood and Leakey (2011), Grine *et al.* (2019), and Schrenk *et al.* (2015) included OMO 75-1969-14 in a taxonomic table, but did not discuss the specific morphological attributes that were used to reach that conclusion. Suwa *et al.* (1996) discussed the large postcanine size that is reminiscent of robust hominins, and note the reduction in the size of the M₃, the latter of which has been argued as a characteristic of *H. habilis sensu stricto* (Wood 1991; although the conclusiveness of this generalization is critiqued by Suwa *et al.* 1996: 273). Instead, Suwa *et al.* (1996) focused on the morphology of the mandibular premolars, especially the P₃, to associate OMO 75-1969-14 with their non-robust taxonomic category. When eight features were subjected to multidimensional scaling, Suwa *et al.* (1996) found that they differentiated robust and non-robust P₃s entirely, and P₄s similarly but to a lesser degree. These features describe the occlusal surface topography, the development of the talonid, and reduced crown asymmetry in the robust taxa (Suwa *et al.* 1996: 266). Coppens (1980) provided a description of the teeth of OMO 75-1969-14, noting a few features that are similar to *Au.*

africanus from Sterkfontein. He also notes that the mandibular bodies of OMO 75-1969-14 and L 860-2 are “somewhat robust, with an inner mandibular arch in V, a symphysis tilted backward with a moderate planum alveolare, developed superior and inferior transverse tori, especially the superior one” (Coppens 1980: 215).

The mixed conclusions for the taxonomic affinity of OMO 75-1969-14 offer a cautionary tale about the difficulty of identifying hominin taxa based on complete mandibles, and even more difficulty when doing so based solely on isolated teeth. We also note the caveat that our analysis relies heavily on linear dimensions, an approach that is efficient and quantitative, but clearly overlooks a considerable amount of information embedded in the morphology.

The dilemma for paleontologists is figuring out how to decipher evolutionarily meaningful anatomical variation from the “noise” of idiosyncratic, normal variation within a population or species (Hlusko 2004, 2016). Genetics-based approaches to re-defining anatomic variation offer a solution, although this work is laborious and proceeding gradually. For example, Hlusko *et al.* (2016) used quantitative genetic analyses to define two ratios that capture the phenotypic variation of genetic influences on the primate postcanine dentition. These genetically-defined traits show strong phylogenetic signals across mammals (Monson *et al.* 2019). When applied to hominins specifically, one of these ratios, the molar-module-components (MMC), reveals a distinction between *Australopithecus* (including *Paranthropus*) and *Homo* (Brasil *et al.* 2020). The MMC of OMO 75-1969-14, defined as the MD dimension of the M₃ divided by the MD dimension of the M₁, is 0.95. This value is outside the range of variation observed in *Australopithecus* and *Paranthropus*, and is within the range of variation for early *Homo*, *H. erectus*, and later species of *Homo* (Brasil *et al.* 2020). The second ratio, the premolar-molar-module (PMM), is defined in Hlusko *et al.* (2016) as the MD dimension of the M₂ divided by the MD dimension of the P₄. This value for OMO 75-1969-14 is 1.5, a value that plots within the first stdv of *Au. afarensis*, early *Homo*, and *H. erectus* (Brasil *et al.* 2020). Therefore, combining the evidence on the morphological affinities of the two premolars (Suwa *et al.* 1996), and the quantitative genetics-defined traits (Hlusko *et al.* 2016; Brasil *et al.* 2020), we conclude that the OMO 75-1969-14 dentition is most appropriately assigned to *Homo* (Table 2).

OMO 75/i-1970-1255 is a right P₃. The BL dimension of this crown cannot be measured because the mesiobuccal aspect of the protoconid is broken. However, the MD dimension plots within the first stdv of *Homo* EEA and *P. aethiopicus* (Fig. 4A). The morphology of the crown is clearly not *Paranthropus*, in that the cusps are less mesially positioned and the talonid is not as extended (following Suwa *et al.* 1996). Therefore, we assign this crown to *Homo* (Table 2).

OMO 75/S-1969-15 is a left M₁ (Howell & Coppens 1974; Suwa *et al.* 1996). This is a smaller tooth than the M₁ of OMO 75-1969-14, with linear dimensions that plot within the first stdv of *Australopithecus* LP and *Homo* EEA (Fig. 6A-C). The shape ratio is very similar to OMO 75-1969-14 (Fig. 6D). The LDA predictions are *Homo* (58%) and *Australopithecus* LP (37%) (Table 8). On the LDA graph, this tooth plots within the dense cluster of comparative specimens of *Australopithecus* LP and *Homo* EEA (Fig. 16). Although this molar shows a worn occlusal surface, we can distinguish a middle and distal trigonid crest interrupted by the central sulcus and a Y-groove pattern. The hypoconulid is very large and there is a small metaconulid. Our designation is similar to that reached by Suwa *et al.* (1996), we attribute it to cf. *Homo* (Table 2).

OMO 75/S-1969-16 is a right M₃ (Howell & Coppens 1974; Suwa *et al.* 1996). The linear measurements of this crown plot at the lower end of the range of variation for *Australopithecus* LP, *Au. anamensis*, *Homo* EEA, and the middle or upper end of the range of variation for *H. erectus* (Fig. 8A-C). The shape ratio is in the overlap of *Australopithecus* LP, *Au. anamensis*, *Homo* EEA, and *P. boisei*, and the upper end of the range of variation observed for *H. erectus* (Fig. 8D). Our LDA predictions are *Homo* (58%) and *Australopithecus* LP (39%) (Table 8). On the LDA graph, the LD1 and LD2 values (-1.08, 0.36; Supplemental Table S9), plot within a dense cluster of comparative specimens attributed to *Homo* EEA, *H. erectus*, and *Australopithecus* LP (Fig. 18). Regarding its morphology, this lower molar has a pronounced anterior fovea and a discontinuous middle and distal trigonid crest. The hypoconulid and metaconulid are small and the entoconulid has the aspect of an enamel wrinkle. There is a pit in the buccal groove of the protoconid. Suwa *et al.* (1996) conclude that this specimen is similar to *Homo* sp. indet. We similarly assign this specimen to *Homo* (Table 2).

OMO 136-1972-1 is a left M₃ with a completed crown and only partial root formation (Howell & Coppens 1974; Suwa *et al.* 1996). This lower molar exhibits a faint anterior fovea and a discontinuous middle and distal trigonid crest. The hypoconulid is small and the entoconulid is moderate. A secondary groove extends across most of the buccal surface of the protoconid. The position of the buccal cusps is relatively more lingual, such that the occlusal fovea appears more closed, a trait associated with *Paranthropus* (character 3, Table 6). There is a strong protoconid shelf. The linear dimensions are just beyond the range of variation observed for *Australopithecus* LP, only overlapping with values observed for *Paranthropus* (Fig. 8A-C). The LDA predictions are *Paranthropus* (56%) and *P. boisei* (49%) (Table 8). On the LDA graph, the LD1 and LD2 values (1.74, 0.42; Appendix 2) plot within the *Paranthropus* polygon, just outside that of *Australopithecus* LP (Fig. 18). Our taxonomic determination for this tooth is *Paranthropus*, aligning with that of Suwa *et al.* (1996), who concluded that this crown is similar to *P. boisei* (Table 2).

OMO 136-1972-2 is a left M_2 (Suwa *et al.* 1996; originally identified as an M_3 lacking the hypoconulid, Howell & Coppens 1974). The linear dimensions plot with the larger specimens of *Homo* EEA and *Australopithecus* LP, and the smaller specimens of *Paranthropus* (Fig. 7A-C). The shape ratio is most similar to the mean observed for *Homo* EEA, but overlaps the observed ranges of variation for *Australopithecus* LP, *H. erectus*, and both species of *Paranthropus* (Fig. 7D). The LDA predictions are *Australopithecus* (58%) and *Homo* EEA (61%) (Table 8). On the LDA graph, OMO 136-1972-2 plots in the overlap between *Homo* EEA and *P. aethiopicus* (Fig. 17). The clustering analysis of morphological scores was not possible for this tooth because it did not have all external features available. The wear on this crown is asymmetrical like a non-robust hominin. Even though the buccal cusps are almost worn flat, there is no dentine exposure, suggesting particularly thick enamel. This crown was determined to have affinities to *P. boisei* by Suwa *et al.* (1996). Weighing the BL dimension similarity to *P. aethiopicus* alongside the shape ratio similarity to *Homo* EEA, the wear pattern, and the enamel thickness inferred from the wear, we agree with Suwa *et al.* (1996) and assign this crown to cf. *Paranthropus* (Table 2).

OMO 195-1973-1630 is a moderately, asymmetrically worn right M_1 with relatively small linear dimensions that are at the lower end of the ranges of variation observed for *Australopithecus* LP, *Au. anamensis*, *Homo* EEA, and *H. erectus* (Fig. 6A-C). The shape ratio plots among the highest values observed for *Australopithecus* LP, *H. erectus*, and *P. boisei*, but falls within the first stdv of *Homo* EEA (Fig. 6D). The crown is classified as *Homo* (76%) and *Homo erectus* (40%) in our LDA (Table 8). On the LDA graph, it plots within a dense cluster of comparative specimens assigned to *Homo* EEA, *Australopithecus* LP, and *H. erectus* (Fig. 16). Because of the degree of wear, this tooth was not scored for our morphological scores cluster analysis. Our taxonomic designation is similar to the noted affinity to *Homo* sp. indet. of Suwa *et al.* (1996), as we assign it to *Homo* (Table 2).

Member H (1.91 Ma to 1.78 Ma)

Two specimens derive from Member H and both are attributed to *Homo* or cf. *Homo* (Table 2). One tooth was recovered by the IORE and the other by OGRE.

OMO 74-1969-18 is an incompletely formed right P_4 (Howell & Coppens 1974). The MD dimension plots within the overlap of all the comparative taxa except for *Ar. ramidus* and *H. erectus* (which are smaller) and *P. boisei* (which is larger) (Fig. 5A). Because we cannot measure the BL dimension reliably, we only include this specimen in the morphological scoring. The crown has a strong mesial fovea, an expanded talonid, and the metaconid and protoconid are not connected by a crest, but rather are separate. There is a disto-buccal cusplet with a free apex. We categorize this tooth as cf. *Homo* (Table 2).

OMO VE 3-10011 is a left M₃. MD and BL dimensions could not be measured on this tooth. This specimen is only included in the morphological scoring. This heavily crenulated, unworn tooth presents a discontinuous middle and distal trigonid crest, a thin mesial marginal ridge and a Y-groove pattern. The hypoconulid and entoconulid are moderate in size. We assign this tooth to *Homo* because the hypoconulid is in a distobuccal position (a configuration more common in *Homo*), and it has the MD elongation that is more suggestive of *Homo* (Table 2).

Member J (1.76 Ma to 1.56 Ma)

Only one specimen included in our analysis derives from Member J, more specifically from unit J4. This specimen was recently recovered during OGRE fieldwork.

OMO 352-10086 is a left M₁. This molar has a thick mesial marginal ridge, an interrupted middle and distal trigonid crest, and a cruciform-groove pattern. There is a small hypoconulid and a moderate entoconulid. The linear dimensions are large, plotting within the MD values of *P. aethiopicus* and *P. boisei*, and above the observed range of variation for BL and MDxBL (Fig. 6A-C). The shape index is low, plotting below the observed range for *P. boisei* (Fig. 6D). The LDA predictions are *Paranthropus* (99.9%) and *P. boisei* (99.9%) (Table 8). On the LDA graph, this specimen plots near the center of the *P. boisei* polygon (Fig. 16). We attribute this specimen to *P. boisei* (Table 2).

Member K (1.53 Ma to 1.39 Ma)

There are three specimens from Member K. One is assigned to *Paranthropus* and two are assigned to *Australopithecus* LP/*Homo* EEA (Table 2).

F 203-1 is a right M₂ (following Suwa 1996; the crown was originally identified as a right M₃, Howell & Coppens 1974). This tooth has a thick mesial marginal ridge enclosing a faint linear anterior fovea and a discontinuous middle trigonid crest. There is an X-groove pattern and a moderately-sized hypoconulid and entoconulid. Grine *et al.* (2019) assigned this tooth to *P. boisei* but identified it as a M₃. The LDA predictions are *Australopithecus* (60 %) and *Australopithecus* LP (44%) (Table 8). Because the crown is worn flat, and has a relatively large hypoconulid and C6, we assign this tooth to *Paranthropus* as well (Table 2).

OMO 343-10001 is a left M³ missing most of the mesiobuccal cusp. The MD and BL dimensions are estimated. The MD dimension falls within the first stdv of *Australopithecus* LP and *Homo* EEA. The BL dimension plots within the first stdv of *Australopithecus* LP and among the largest dimensions observed for *Au. anamensis*, *Ar. ramidus*, *H. erectus*, and *Homo* EEA. Morphologically, the crown lacks features

associated with *Paranthropus*, but does not demonstrate any morphology that would differentiate between *Australopithecus* and *Homo*. Therefore, we attribute this specimen to *Australopithecus* LP/*Homo* EEA (Table 2).

OMO 362-10039 is a right P⁴. Morphologically, this unworn, crenulated P⁴ exhibits distal and mesial accessory ridges and a marked groove on the distobuccal surface. The buccal essential crest is single and the lingual one is bifurcated. The linear dimensions plot within the overlap of *Australopithecus* LP, *Au. anamensis*, and *Homo* EEA (Fig. 10A-C). The shape index similarly overlaps with almost all the comparative taxa (Fig. 10D). The LDA predictions are *Australopithecus* (72%) and *Australopithecus* LP (58%) (Table 8). On the LDA graph, this specimen plots in a cluster of comparative specimens that represent *Australopithecus* LP and *Homo* EEA (Fig. 15). We assign this tooth to *Australopithecus* LP/*Homo* EEA (Table 2).

Member L (1.38 Ma to ca. 1.09 Ma)

There are five specimens from Member L. Four of these specimens are recent discoveries by the IORE project. All but one specimen are attributed to *Homo*, *H. erectus*, or cf. *Homo* (Table 2). The fifth specimen is attributed to *Paranthropus*, and represents the geologically youngest *Paranthropus* recovered from the Omo to date.

OMO 342-10126b is the germ of a right M₁ associated with a mandibular fragment with the roots of dp₄. This lower molar shows a pronounced mesial fovea with a thin mesial marginal ridge and a discontinuous middle and distal trigonid crest. The hypoconulid is small and the groove pattern is cruciform, a more derived configuration that is associated with *Homo*. In terms of linear dimensions, this tooth plots within the overlap zone of *Australopithecus* LP, *Au. anamensis*, *Homo* EEA, and *H. erectus* (Fig. 6A-C). The shape index is most like *Homo* EEA (Fig. 6D). The LDA predictions are *Homo* (68%) and *H. erectus* (40%) (Table 8). On the LDA graph, this specimen plots within the dense cluster of comparative specimens from *Australopithecus* LP, *Au. anamensis*, *Au. deyiremeda*, *Homo* EEA, and *H. erectus* (Fig. 16). We attribute this M₁ to the genus *Homo* (Table 2).

OMO 382-10008 is the distal aspect of a left M³. Not enough of the crown is preserved to take MD or BL measurements, however the crown is obviously large with the closed occlusal fovea characteristic of *Paranthropus* and thick enamel. This specimen represents the geologically youngest *Paranthropus* in the Omo (Table 2).

OMO 383-10124 has two dental elements preserved, a fragment of a left M¹ (OMO 383-10124a) and a left M² (OMO 383-10124b). The MD, BL, and MDxBL dimensions of the M¹ plot within the first stdv of

Australopithecus LP, *Au. anamensis*, and *H. erectus* (Fig. 11A-C). On the LDA graph, this M¹ plots in the overlap of the *Homo* EEA, *H. erectus*, and *Australopithecus* LP polygons (Fig. 16). The LD predictions are *Homo* (75%) and *H. erectus* (37%) (Table 8). The linear dimensions of the M² overlap consistently with *Homo* EEA, and the shape index similarly overlaps with the first stdv of both *Homo* EEA and *H. erectus* (Fig. 12A-D). On the LDA graph, this specimen plots within the center of both the *Homo* EEA and *H. erectus* polygons, within the *Australopithecus* LP polygon, and along the edge of the *Au. anamensis* polygon (Fig. 17). The LDA predictions for the left M² are *Homo* (58%; note that the prediction for *Australopithecus* is 38%) and *H. erectus* (37%) (Table 8 and Supplemental Table S8). We assign both teeth to *H. erectus* (Table 2).

OMO 389-10085 is a worn right M₃. The clustering analysis was not possible for this tooth because all external features were not observable. The linear dimensions of this crown all plot with the smaller specimens of *H. erectus* (Fig. 8A-C). The shape index plots alongside the smallest specimens of *Ar. ramidus*, *Australopithecus* LP, and *Homo* EEA, and among the smaller specimens of *H. erectus* (Fig. 8D). The LDA predictions are *Homo* (60%) and *H. erectus* (67%) (Table 8). On the LDA graph, this specimen plots in the center of the *H. erectus* polygon, overlapping that of *Ar. ramidus* (Fig. 18). We assign this tooth to *H. erectus* because of the LDA predictions and because the distal aspect is very reduced, a characteristic much more similar to *Homo* than other hominin taxa (Table 2).

OMO K 7-1969-19 is a left M₂ (Howell & Coppens 1974; identified as an M₁ by Suwa 1996). The M₂ presents a very large hypoconulid and a medium-sized metaconulid, a Y-groove pattern and a moderate protostylid. The hypoconulid is distobuccally oriented, a configuration more common in *Homo* than in other hominins. The MD dimension plots within the *Homo* EEA first stdv and overlaps with larger specimens of *Australopithecus* LP (Fig. 8A). The BL dimension plots on the mean for *H. erectus*, and overlaps with smaller specimens of *Homo* EEA and *Australopithecus* LP (Fig. 8B). The MDxBL value is within the first stdv of *Australopithecus* LP, *Au. anamensis*, and *Homo* EEA, and among the larger values for *H. erectus* (Fig. 7C). The shape index is one of the highest values observed, overlapping with the highest values for *Australopithecus* LP, *H. erectus*, and *P. aethiopicus* (Fig. 7D). The LDA predictions are *Homo* (61%) and *Homo* EEA (40%) (Table 8). On the LDA graph, this specimen plots just outside of the overlap between the polygons of *Homo* EEA, *H. erectus*, and *Australopithecus* LP (Fig. 17). We assign this specimen to cf. *Homo* (Table 2).

1792

1793 DISCUSSION

1794

1795 The aim of this study is to provide the most specific taxonomic identifications possible for the Omo dental
1796 specimens. Using a combination of quantitative methodologies and qualitative assessments, we present
1797 a detailed evaluation of each tooth in comparison with a large dataset of hominin teeth. Our final
1798 taxonomic determinations are presented in Table 2. We summarize the taxonomic identification by
1799 stratigraphic level in Table 10.

1800

1801 The implications and hypotheses that these identifications raise will be explored in detail in future
1802 publications. Perhaps the most poignant conclusion we can make at the end of this lengthy taxonomic
1803 exercise is the same as the conclusion reached by John T. Robinson in 1956, "...it obviously is not wise to
1804 rely entirely on evidence of one sort alone because the understanding of an animal—hence also its
1805 classification—must depend on as complete a study as material and opportunity allow... Classification
1806 simply serves as a means of simplifying discussions by providing a set of labels and at the same time is a
1807 brief and specialized sort of summary of the results of trying to understand animals and their evolution"
1808 (1956: 167). Robinson was skeptical of how much our taxonomic inferences should lean on dental
1809 variation alone, especially because parallelism or convergence among closely related animals may be a
1810 serious confounding factor (Robinson 1956:167). And with that said, we ask the reader to use our
1811 identifications in Table 2 with caution.

TABLE 10. – Summary of Omo taxonomic assignments by stratigraphic level*.

Strat Level	Age** (Ma)	<i>Au. LP</i>	<i>Au. garhi</i>	<i>Au. LP/ Homo EEA</i>	<i>Homo</i>	<i>H. erectus</i>	<i>Paranthropus</i>	<i>P. aethiopicus</i>	<i>P. boisei</i>	Total
L	1.4 - 1.05				2	2	1			5
K	1.5 - 1.4			2			1			3
J	1.77 - 1.5								1	1
H	1.9 - 1.77				2					2
G	2.27 - 1.9			1	8		10		3	23 [^]
F	2.32 - 2.27		1	6	6		1	6		20
E	2.4 - 2.3	1		3			1	2	1	8
D	2.5 - 2.4			2			2			4
C-4 - C-9	2.7 - 2.5			15	1***		1	5		22
B-9 - C-1	2.95 - 2.9	2		5			3			10
B-2	3.4	8		2						10

*Includes comparative specimens.

** Approximate geologic age.

*** This specimen was found near a fault, and could be either from Member C or Member F.

[^]Includes a specimen identified only to hominin.

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1842

1843 **AUTHOR CONTRIBUTIONS**

1844 **Leslea J. Hlusko:** lead the research, described and measured the specimens, created the comparative
1845 dataset, obtained the grant funding, wrote the manuscript and SOM

1846 **Franck Guy:** described and photographed the specimens, provided significant assistance with logistics,
1847 edited multiple versions of the manuscript

1848 **Mario Modesto-Mata:** designed and implemented the LDA and wrote this section of the manuscript,
1849 performed the two hierarchical analyses, was primarily responsible for creating figures 4-22

1850 **Marina Martinez de Pinillos:** described the specimens, collected the data for the study of morphological
1851 scores and wrote this section of the manuscript, edited an earlier version of the manuscript

1852 **Marianne F. Brasil:** conducted all analyses of the linear metrics from the comparative dataset, created
1853 figure 2, significantly edited multiple versions of the manuscript

1854 **Ian Towle:** collected the data for the cusp area study and wrote this section of the manuscript, edited an
1855 earlier version of the manuscript

1856 **Arthur Thiebaut:** created figure 1, significantly edited an earlier version of the manuscript

1857 **Jean-Reanaud Boisserie:** directed the OGRE fieldwork that the recovered the fossils, provided significant
1858 assistance with logistics, obtained the grant funding, significantly edited multiple versions of the
1859 manuscript

1860

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Taxonomic assignments for the 3.4 Ma to 1.1 Ma hominin postcanine teeth from the Usno Formation and the Shungura Formation, Lower Omo Valley, Ethiopia

Attributions taxinomiques de la denture jugale des hominines des formations d'Usno et de Shungura (3,4 Ma – 1,1 Ma), basse vallée de l'Omo, Éthiopie

Leslea J. Hlusko, Franck Guy, Marina Martinez de Pinillos, Mario Modesto-Mata, Ian Towle,
Marianne F. Brasil, Arthur Thiebaut, Jean-Reanaud Boisserie

Supplementary Materials

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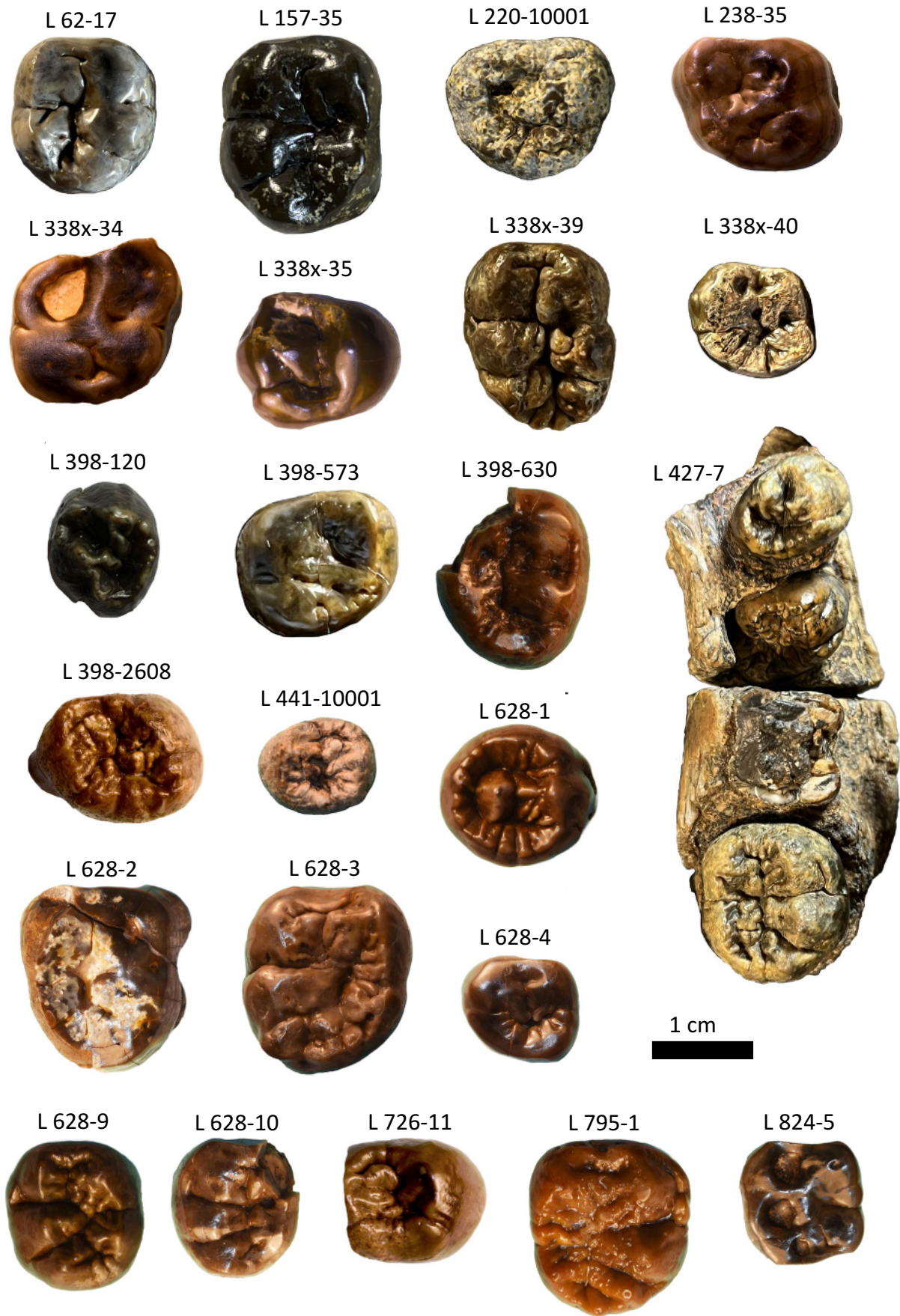
Supp. Fig. S1. Occlusal views of Omo hominin specimens, plate 1 of 7



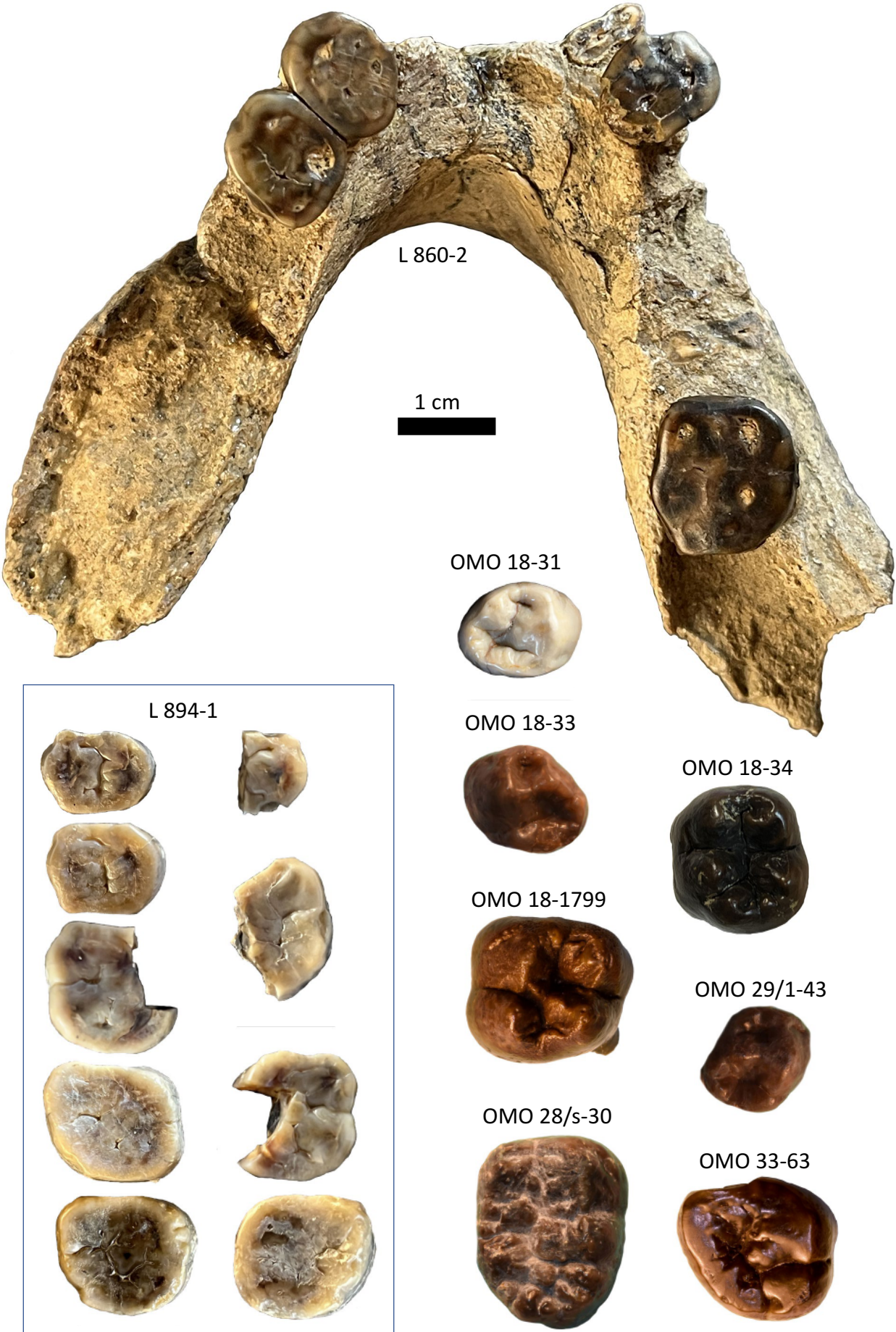
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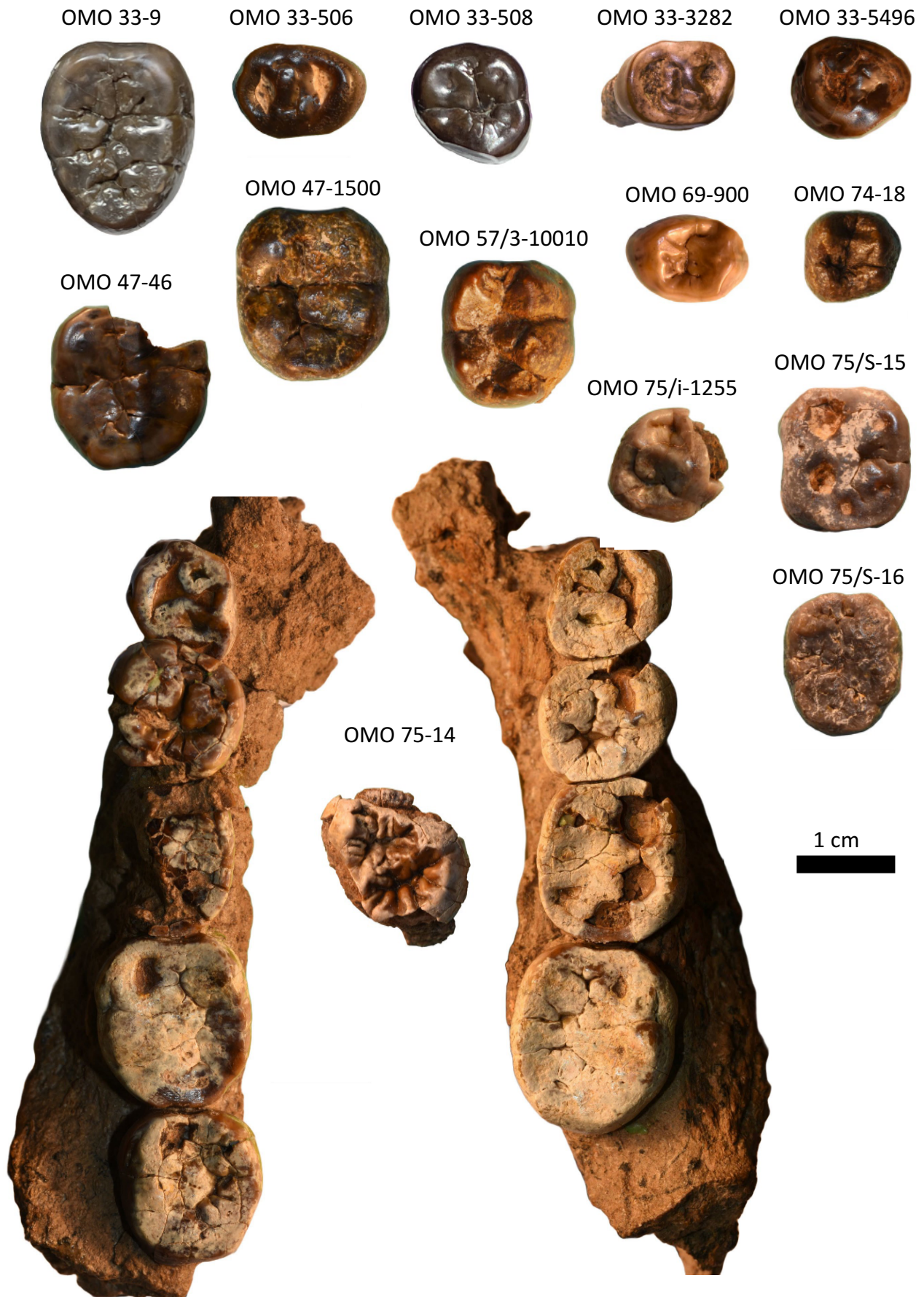
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Supp. Fig. S1. Occlusal views of Omo hominin specimens, plate 4 of 7



Supp. Fig. S1. Occlusal views of Omo hominin specimens, plate 5 of 7



Supp. Fig. S1. Occlusal views of Omo hominin specimens, plate 6 of 7



Supp. Fig. S1. Occlusal views of Omo hominin specimens, plate 7 of 7

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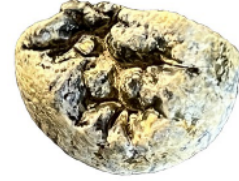
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OMO 371-10035



OMO 382-10008



OMO 383-10124a



OMO 383-10124b



OMO 389-10085



OMO K 7-19



OMO SH 1/1-17



OMO VE 3-10011



P 933-1



W 7-23



W 7-508



W 8-749



W 8-752



W 8-988



W-978



1 cm



