

Readjustment of the Standard ASUDAS to Encompass Dental Morphological Variations in Plio-Pleistocene Hominins

Précision du système de référence ASUDAS pour prendre en compte la variation morphologique des hominines plio-pléistocènes

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Abstract The standard ASUDAS scoring system (Arizona State University Dental Anthropology System) is used to assess dental morphological variations in modern humans. It is also frequently used to study, score, and compare morphological variations in fossil hominin taxa and to examine their phylogenetic relationships. However, using ASUDAS in studies of this type is under debate because it is based on modern *Homo sapiens* populations and does not appear to cover all variations observed in fossil Plio-Pleistocene hominins. Our observations and coding of 178 dentals casts of Plio-Pleistocene specimens based on ASUDAS and from the literature have confirmed the need to adapt the standard system to fossil hominins. In this initial study, we propose that the scoring procedures for some morphological characters need to be readjusted, while others could be standardized following the ASUDAS system.

Keywords Dental morphology · Plio-pleistocene hominins · ASUDAS

Résumé Le système de codage de référence des caractères morphologiques dentaires ASUDAS (Arizona State University Dental Anthropology System) est un outil fréquemment utilisé pour étudier, coder et comparer les différents groupes d'hominines fossiles. Or, ce système étant basé sur des populations d'hommes actuels, il ne couvre pas l'ensemble de la variation morphologique observée sur les hominines plio-pléistocènes. Une adaptation du système de référence à ces derniers permettrait de renforcer la pertinence de son utilisation dans les études paléanthropologiques. Suite à l'examen morphologique et au codage d'un échantillon de 178 moulages dentaires de spécimens plio-pléistocènes selon les plaques ASUDAS et les données de la littérature, nous avons pu

confirmer la nécessité d'adapter le système de référence ASUDAS. Dans cette première étude, nous montrons que certains caractères morphologiques nécessitent un réajustement de leurs procédures de codage et que d'autres peuvent faire l'objet d'une standardisation sur le modèle ASUDAS.

Mots clés Morphologie dentaire · Hominines plio-pléistocènes · ASUDAS

Introduction

The Arizona State University Dental Anthropology System (ASUDAS) is frequently used in taxonomic and phylogenetic studies on fossil hominins [1,2]. Published in 1991 by G. Richard Scott and Christy G. Turner II, ASUDAS covers > 30 characters considered to be representative of morphological variations in modern *Homo sapiens* [3–5]. The authors describe discrete dental characters and their grades of expression. For most of the characters, scoring is easier with the reference plaque, which represents the different grades of expression. This system is particularly useful because it makes it possible to standardize scoring, thus facilitating comparisons between morphological studies: the primary purpose of the standard ASUDAS is in fact to standardize the scoring of morphological characters that are easily and reliably observable. In addition, when taken together, these traits can be used to characterize populations [3]. Therefore, dental morphological traits may be relevant either to distinguish between geographic populations within a species, or to distinguish between taxa at a higher level [1,6].

This scoring system has also been used to describe dental morphological variations in fossil hominins. However, some studies consider that it may not be appropriate for morphological descriptions of fossil hominin teeth [1,2,6,7] because it is based on modern human populations (initially, mainly

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Native South American and Arctic populations) [4,5]. Therefore, it seems important to test whether ASUDAS can encompass the wide morphological variations found in the different Plio-Pleistocene hominin species.

Many studies have described the dental morphology of fossil specimens and estimated how dental morphological variations were distributed across fossil hominin taxa [e.g.], [8,9]. However, since the publication of ASUDAS [3] and apart from uploaded versions [4,5], very few authors have attempted to adapt the system or to propose new standards that would be required for studies of fossil hominins [2,6,7,10–14]. This paper reports on our study to test whether ASUDAS is appropriate to the morphological coding of Upper Pliocene and Lower Pleistocene hominins, and to propose possible readjustments to the system.

Materials and Methods

The initial sample was made up of a collection of more than 200 high-resolution silicone (©President light body) dental crown casts belonging to Sandrine Prat. Because postcanine teeth have a larger number of morphological characters than canines and are less subject to sexual dimorphism, this study focused on premolars and molars. The specimens are from Upper Pliocene and Lower Pleistocene South and East African sites (mainly Sterkfontein, Swartkrans and the Omo valley). One specimen from Dmanisi (D 211) was also included in the study. The taxa in our sample are *Australopithecus*, *Paranthropus* and early *Homo* (Table 1).

From the initial collection, we selected maxillary and mandibular premolars and molars. We excluded third molars because of their complex and irregular morphology. Teeth with limited wear or fragmentation (i.e., on which we were able to observe and score at least one character) were included in the study. We thus used a sample of 178 teeth: 34 upper premolars, 41 upper molars, 43 lower premolars, 60 lower molars (Table 1).

We scored 22 characters following the standard scoring procedure developed by Scott and Turner [3–5]. We also included 11 additional, or revised, characters described in the literature after the publication of ASUDAS in 1991 [2,6,7,10–14]. These studies described the types of expression of some additional characters that were relevant to morphological descriptions of fossil hominins and were not included in ASUDAS [3–5]. The authors [2,6,7,10–14] proposed descriptions and standardizations to complement ASUDAS, but usually with no reference plaques. We did not take taxonomic attribution into account during our observations in order to minimize observer subjectivity, and we did not analyze and describe characters that appeared to be constant in our sample (Table 2). Concerning the revised or new characters presented in this study, we tested both intra-

observer variability (scored three times by M.L.) and inter-observer variability (scored by S.P. and M.L.). Inter-trait correlations were estimated with Kendall's τ test using only one tooth from each district. The frequencies of dental traits are provided for each taxon in our sample. Specimens with uncertain taxonomic attribution, as for “non-robust” specimens, are not counted in the trait frequencies. The distribution of frequencies between taxa is estimated and compared by means of a Fisher exact test, as the very small samples prevented us from applying a chi-squared test. Groups with < 2 specimens were not included in the Fisher exact test.

Results and discussions

We propose an initial approach for several dental characters and additional grades for existing traits that would allow more accurate assessments of dental morphological variations in Plio-Pleistocene hominins, and a standardization of their scoring procedures. We observed that 19 ASUDAS characters are well suited to studies focusing on Plio-Pleistocene hominins (Table 2), which means that the standard system can be used to score Plio-Pleistocene hominins. Three ASUDAS characters needed a readjustment of their scoring procedures (Table 3). A new scoring procedure for the protostylid is proposed, to combine the ASUDAS reference plaque and the types of expression described by Hlusko [7] (see below). Seven additional characters are well suited when applied to Plio-Pleistocene hominins (Table 4). We argue that three characters already described in the literature (Table 5) are observed in particular in Plio-Pleistocene hominins [6,14] and should therefore be integrated into the standard system with their initial scores. This study also proposes descriptions and scoring procedures for three new characters (Table 6), including disto-buccal cusplets on lower premolars as described in Suwa's thesis on upper premolars.

With regard to intra- and inter-observer errors, we found very high replicability for a single observer and no less than 77% replicability between the two authors. No significant differences were apparent. Inter-observer errors were estimated at 88% and 98% for disto-buccal cusplets on upper and lower premolars, respectively, 93% for hypocone reduction, >99% for double cusp 5, 81% for the distal fovea, 80% for the hypoconulid, 89% for the protostylid, 98% for double cusp 6, and 77% for the mesial marginal ridge. Concerning inter-trait correlations, most significant correlations ($p < 0.05$) do not exceed $\tau = 0.4$ or -0.4 (LM1 double cusp 6 and mesial marginal ridge, LM1 mesial marginal ridge and cusp 7, LM1 mesial marginal ridge and deflecting wrinkle, LM1 hypoconulid and Y-pattern, LM1 mesial marginal ridge and protostylid, LM2 double cusp 6 and cusp 6, UM1 distal fovea and crista obliqua, LM2 cusp 5 and cusp 7, UM1 double cusp

Table 1 List of Plio-Pleistocene hominins studied in this paper / <i>Liste des hominines plio-pléistocènes étudiés dans cet article</i>				
<i>Au. afarensis</i> and aff. <i>afarensis</i>		<i>Au. africanus</i>		
AL 128–23	RP ₃	MLD 2	LM ₁	
	RP ₄		LM ₂	
	RM ₁	Sts 8	LM ¹	
	RM ₂		LM ²	
AL 145–35	LM ₁	Sts 9	RM ₁	
	LM ₂	Sts 24	LP ³	
AL 199–1	RP ³		LM ¹	
	RP ⁴		LP ₃	
	RM ¹		RM ₁	
	RM ²	Sts 51	RP ₃	
AL 200–1a	LP ³	Sts 55	LP ³	
	LP ⁴	Sts 56	LM ¹	
	LM ¹	Stw 151	LM ₁	
	LM ²	Stw 252	LP ³	
AL 333w–1b	RP ₄		LP ⁴	
	RM ₁		LM ¹	
	RM ₂		LM ²	
B7–39A	LP ³	Taung 1	LM ₁	
B7–39B	LP ⁴	TM 1511	RP ³	
B7–39C	LM ¹	TM 1523	LP ₄	
B8–23A	LP ⁴			
B8–23B	LM ¹			
B8–4q	LP ⁴			
B8–49	LP ⁴			
LH 2	RM ₁			
W7–23	LP ₄			
W7–508	RM ₁			
W8–751	LP ₄			
W8–978	RP ₃			
W8–749	RM ^{1 or 2}			
W8–988	LP ⁴			
<i>Au. bahrelghazali</i>				
KT1	LP ₃			
	LP ₄			
<i>P. aethiopicus</i>		<i>P. boisei</i>		
F22–1a	RM ₂	L628–9	LM _{1 or 2}	
L51–79	RP ₄	L628–10	LM ₁	
L62–17	RM ₂	L726–11	RP ³	lingual fragment
L338x35	RP ³	WT 37747	RM ¹	
L338x40	LP ₄	WT 47844	RM ₁	
L398–120	RP ₃	lingual fragment		
L398–1223	RP ₄	lingual fragment		
L420–15	LP ₄	buccal fragment		
L465–111	LP ₃			
Omo 18–68–31	RP ₃			
Omo 18–68–33	LP ₃			

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Table 1 (<i>suite</i>)				
Omo 18-68-34	LM ₁ or 2			
Omo 18-70-1799	LM ¹			
Omo 33-71-508	LP ₄			
Omo 136-2	LM ₂ or 3			
<i>P. robustus</i>		<i>Early Homo</i>		
SK 1	LM ₂	K7-19	LM ₂	
SK 6	LP ₄	L26-1G	LM ₂	
	LM ₁	OH 7	LP ₃	
	LM ₂		LP ₄	
SK 7	RP ₄		LM ₁	
SK 9	LP ₄		LM ₂	
SK 24	LP ³	OH 13	RP ³	
SK 33	RP ³		RP ⁴	
SK 61	RM ₁		LM ¹	
	RM ₂		LM ²	
SK 88	LP ₄	OH 21	LM ¹	Germ
SK 89	LM ¹	OH 22	RP ₃	
SK 98	LM ²		RP ₄	
SK 102	LM ¹		RM ₁	
SK 104	RM ₁		RM ₂	
SK 823	RP ³	Omo 29-1968-43	RP ₃	
SK 824	LP ⁴	Omo 74-18	RP ₄	
SK 825	LP ⁴	Omo 123N-1973-5495	RP ₃	
SK 831	RP ₃	Omo 177-4525	RP ₃	
SK 832	LM ¹	Omo SH1-1-17	LM ¹	
SK 834	RM ²	P933-1	LM ¹	
SK 835	LM ²	SE 255	RM ¹	
	RM ₁	SK 15	RM ₁	
	RM ₂		RM ₂	
SK 837	RM ²	SK 27	LP ³	
SK 843	LM ₁		RM ²	
	LM ₂	SKW 3114	LM ²	
SK 857	RP ₃	SKX 258	LM ₁	
SK 3974	RM ₁	SKX 268	RM ¹	
SK 3976	LM ₂	WT 42718	RM ₁	
SK 13114	RP ³	WT 47767	LM ²	
	RP ⁴			
	LM ¹			
	RM ²			
SK 1587a	LP ₄			
	LM ₁			
	LM ₂			
SKW 5	RP ₃			
	RP ₄			
	RM ₁			
	RM ₂			
SKW 4767	RM ₁			
SKW 4772	RP ⁴			
SKW 14129	RM ¹			

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Table 1 (<i>suite</i>)			
SKX 162	RP ³		
	RP ⁴		
SKX 4446	RP ₄		
	RM ₁		
	RM ₂		
SKX 26625	LP ⁴		
TM 1517	LP ³		
	LP ⁴		
	LM ¹		
	LM ²		
	LP ₃		
	LP ₄		
	RM ₁		
	RM ₂		
<i>H. georgicus</i>		<i>Uncertain</i>	
D211	LP ₃	KB 5223	RM ²
	LP ₄		LM ₁
	LM ₁	L28–31	RM _{1 or 2}
	LM ₂	L45–2	RM _{1 or 2}
		L50–2	LM ^{1 or 2}
		L51–1	LM ₁
		L51–2	LM ^{1 or 2}
		L51–4	LM ^{1 or 2}
		L51–80	RP ₄
		L795–1	RM _{2 or 3}
		Omo 69–900	LP ⁴
		Omo 212–1950	LM ₁

5 and cusp 5, LP4 disto-buccal cusplet and metaconid placement, UP4 disto-buccal cusplet and accessory marginal tubercles). Those ranging from (-)0.4 to (-)0.6 are not judged to be high enough to discard any character [5] (LM1 double cusp 6 and cusp 6, LM1 double cusp 6 and cusp number, LM1 mesial marginal ridge and cusp 6, LM1 mesial marginal ridge and cusp number, LM2 double cusp 6 and deflecting wrinkle, UM1 hypocone and lingual paracone tubercle, LP4 disto-buccal cusplet and mesio-lingual groove, LP4 disto-buccal cusplet and crown asymmetry). The highest significant correlations were found between LM1 cusp 6 and double cusp 6 ($\tau=0.6$, $p=0.00007$) and between cusp 6 and mesial marginal ridge ($\tau=0.6$, $p=0.0002$). The lowest significant correlation was found between LM1 mesial marginal ridge and protostylid ($\tau=-0.3$, $p=0.02$).

Readjustment of scoring procedures for ASUDAS characters

Concerning the readjustment of the scoring procedure, our observations suggest adding a sixth development grade for

two characters: the hypocone on upper molars and the hypoconulid on lower molars. Additional grades described by Hlusko [7] are confirmed for the protostylid expression on lower molars.

Hypocone, upper molars (Table 3)

A large proportion of modern humans show an extreme reduction, and sometimes the complete absence [3], of this distolingual cusp, or hypocone, on upper molars. In our sample, only one molar (e.g., SK 27, *Paranthropus robustus*) shows a significant reduction of this cusp whereas the majority of the sample has either a large or very large hypocone, i.e., grades 4 and 5. In ASUDAS, the expression types are described according to the absolute size of the cusp. However, some Plio-Pleistocene hominins show a fourth cusp that exceeds the size of the grade 5 ($n=17$). We propose to add a sixth development grade described as: “Cusp 4 is much larger than metacone and shows a distolingual projection” (Fig. 1). Because this character is not illustrated in the current ASUDAS although it is observed on several specimens, it should be incorporated into the standard system.

<p>Table 2 List of constant ASUDAS dental characters used in this study [3–5,11] / <i>Liste des caractères morphologiques dentaires ASUDAS constants utilisés dans cette étude [3–5,11]</i></p>
<p><i>Upper premolars</i></p> <p>Disto-sagittal ridge [3–5] Presence of a ridge from the apex of the buccal cusp to the distal occlusal border at the sagittal sulcus Grades: 0 (absence), 1 (presence)</p> <p>Secondary marginal tubercles [3,4] Presence of a secondary mesial or distal tubercle on the marginal ridge 21. Grades: 0 (absence), 1 (presence)</p> <p>Tricuspid premolars [3] Presence of an additional distolingual cusp Grades: 0 (absence), 1 (presence)</p>
<p><i>Lower premolars</i></p> <p>Lingual cusp number [3–5] Number and relative size of lingual cusps Grades: A (absence), 0 (one lingual cusp), 1 (one or two lingual cusps), 2 (two lingual cusps; mesial cusp much larger than distal cusp), 3 (two lingual cusps; mesial cusp larger than distal cusp), 4 (two lingual cusps; mesial and distal cusps equal in size), 5 (two lingual cusps; distal cusp larger than mesial cusp), 6 (two lingual cusps; distal cusp much larger than mesial cusp), 7 (two lingual cusps; distal cusp very much larger than mesial cusp), 8 (three lingual cusps; cusps equal in size), 9 (three lingual cusps; mesial cusp larger than medial and/or distal cusp)</p> <p>Secondary mesial ridge [4,11] Development of a secondary ridge on the mesiolingual border of the tooth Grades: 0 (absence), 1 (presence)</p> <p>Secondary distal ridge [4,11] Development of a secondary ridge on the distolingual border of the tooth Grades: 0 (absence), 1 (presence)</p>
<p><i>Upper molars</i></p> <p>Metacone [3,5] Presence and size of the disto-buccal cusp Grades: 0 (absence), 1 (an attached ridge is present but there is no free apex), 2 (a slight cusplet with a free apex is present), 3 (slight cusp is present), 3.5 (medium-sized cusp), 4 (large cusp), 5 (very large cusp)</p> <p>Parastyle [3–5] Development of a cingular remnant on the buccal surface of the paracone Grades: 0 (absence), 1 (a pit is present in the buccal groove between cusps 2 and 3), 2 (small cusp with an attached apex), 3 (medium-sized cusp with a free apex), 4 (large cusp with a free apex), 5 (very large cusp)</p> <p>Carabelli's cusp [3–5] Development of a cingular remnant on the lingual surface of the protocone Grades: 0 (absence), 1 (a groove is present), 2 (a pit is present), 3 (small Y-shaped depression), 4 (large Y-shaped depression), 5 (small cusp without a free apex), 6 (medium-sized cusp with an attached apex making contact with the medial lingual groove), 7 (large free cusp)</p> <p>Cusp 5 [3–5] Presence and size of a fifth cusp between cusps 3 and 4 Grades: 0 (absence), 1 (slight cusplet), 2 (trace cusplet), 3 (small cusplet), 4 (small cusp), 5 (medium-sized cusp)</p> <p>Secondary mesial marginal tubercles [4] Presence of secondary tubercles on the mesial marginal ridge Grades: 0 (absence), 1 (mesial paracone tubercle), 2 (protoconule), 3 (secondary mesial tubercle), 4 (lingual paracone tubercle)</p>
<p><i>Lower molars</i></p> <p>Groove pattern [3–5] Grades: Y (cusps 2 and 3 are in contact), + (cusps 1 to 4 are in contact), X (cusps 1 and 4 are in contact)</p>

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Table 2 (<i>suite</i>)
<p>Cusp 6 [3–5] Presence and size of the entoconulid, between the hypoconulid and the entoconid Grades: 0 (absence), 1 (cusp 6 much smaller than cusp 5), 2 (cusp 6 smaller than cusp 5), 3 (cusps 6 and 5 equal in size), 4 (cusp 6 larger than cusp 5), 5 (cusp 6 much larger than cusp 5)</p>
<p>Cusp 7 [3–5] Presence and size of cusp 7, or metaconulid, between cusps 2 and 4 Grades: 0 (absence), 1 (slight cusp), 2 (small cusp), 3 (medium-sized cusp) to 4 (large cusp)</p>
<p>Cusp number [3–5] Cusp number does not include cusp 7. Grades: 4 (protoconid, metaconid, entoconid, hypoconid), 5 (with hypoconulid), 6 (with entoconulid)</p>
<p>Deflecting wrinkle [3–5] Presence and shape of the medial ridge on cusp 2 Grades: 0 (absence), 1 (medial ridge is straight but with a midpoint constriction), 2 (medial ridge is deflected distally but does not make contact with cusp 4), 3 (medial ridge is distally deflected forming an L-shaped ridge and comes in contact with cusp 4)</p>
<p>Anterior fovea [3–5] Development of a triangular depression distal to the mesial marginal ridge Grades: 0 (absence), 1 (faint groove), 2 (groove deeper than in grade 1), 3 (groove longer than in grade 2), 4 (groove is very long and mesial ridge is robust)</p>
<p>Distal trigonid crest [3–5] Presence of a ridge connecting the distal borders of cusps 1 and 2 Grades: 0 (absence), 1 (presence)</p>
<p>Mid-trigonid crest [5,10,11,13] Presence and shape of a ridge connecting the mesial aspects of cusps 1 and 2 Grades: 0 (absence), 1 (interrupted crest), 2 (crest forms a complete bridge)</p>

Table 3 List of ASUDAS characters for which scoring procedures need readjustment [3–7] / <i>Liste des caractères ASUDAS nécessitant un réajustement de leurs procédures de codage [3–7]</i>
<i>Upper molars</i>
<p>Hypocone [3–5] Presence and size of the distolingual cusp Grades: 0 (absence), 1 (slight ridging present at the site), 2 (slight cusplet), 3 (small cusp), 3.5 (medium-sized cusp), 4 (large cusp), 5 (very large cusp) Grade 6 (this study): cusp 4 is much larger than metacone and shows a disto-buccal projection</p>
<i>Lower molars</i>
<p>Hypoconulid [3–5] Presence and size of the most distal cusp between cusps 3 and 4 Grades: 0 (absence), 1 (very small cusp), 2 (small cusp), 3 (medium-sized cusp), 4 (large cusp), 5 (very large cusp) Grade 6 (this study): cusp 5 is larger than the hypoconid and the entoconid</p>
<p>Protostylid [3–7] Development of a cingulum derivative on the buccal surface [7], or a paramolar cusp according to the ASUDAS description [3–5]. Grades: 0 (absence), 1 (buccal pit), 2 (very slight swelling), 3 (slight positive expression), 4 (moderate positive expression), 5 (strong positive expression), 6 (pronounced positive expression), 7 (most distinctive form of protostylid, expressed as tubercle) Additional grades ([7], this study): 4A (V-cleft centrally located on the buccal groove. The bottom of the groove is covered with enamel), 4B (robust cingulum parallel to the occlusal surface and centrally located on the buccal groove, with a cusplet frequently observed), 6A (deep linear cleft parallel to the occlusal surface and extending mainly onto the protoconid. The bottom of the buccal groove is covered with enamel), 7A (linear cleft extends onto the mesial border of the protoconid and expands on the buccal side)</p>



Fig. 1 ASUDAS reference plaque, hypocone, upper molars [3–5] and grade 6 (this study). Scoring: grade 0 (absence) to 5 (very large cusp); grade 6 (mirror image of Sts 8, *Au. africanus*, LM2): cusp 4 is much larger than metacone and shows a distolingual projection. Occlusal views. Scale bar = 1 cm / *Plaque de référence ASUDAS pour le caractère hypocone sur les molaires supérieures [3–5] et stade 6 (cette étude). Codage : 0 (absence) à 5 (très large) ; Stade 6 (image en miroir de Sts 8, Au. africanus, LM2) : l’hypocone est plus large que le metacone et présente une projection distolinguale. Vues occlusales. Echelle = 1 cm*

Frequencies of grade 6 for this character are 1/4 for *Australopithecus africanus* M¹ and 2/2 for M² (Table 7). Frequencies for *P. robustus* M¹ are 3/6 and 4/6 for M². It seems less frequent on *Australopithecus afarensis* (1/5 for M¹ and 1/2 for M²) and early *Homo* (2/6 for M¹ and 0/4 for M²) upper molars. With regard to grade 6, we did not find any significant differences between taxa ($p > 0.07$), even for all upper molars and species grouped together ($p > 0.05$).

Hypoconulid, lower molars (Table 3)

Cusp 5, or the hypoconulid, is the most distal cusp and occurs on lower molars between the hypoconid and the entoconid. It is scored according to the absolute size of the cusp and only if cusp 6 is absent. It is variable in size in modern humans and may be absent [3]. However, cusp 5 occurs in all of our samples, the majority at grade 3 (medium-sized) or more. Grade 5 was described by Scott and Turner as “cusp 5 is very large”, but if we try to score our sample against the reference plaque, some molars show a cusp 5 that is larger

than the maximum grade. We therefore suggest adding a sixth grade for this character. To facilitate the scoring procedure and to limit bias arising from the size parameter, grade 6 is described as “cusp 5 is larger than the hypoconid and the entoconid” (Fig. 2). Our results show that grade 6 is mostly observed on *Paranthropus* specimens (Table 7). Among the seven molars with a hypoconulid scored as grade 6, three (2/11 M₁ and 1/9 M₂) are attributed to *P. robustus*, two (2/3 M₁) to *Paranthropus boisei*, one (1/3 M₂) to *Paranthropus aethiopicus* and one (1/3 M₂) to *Au. afarensis*. None of the early *Homo* specimens in our sample have a grade 6 hypoconulid. We did not find any significant differences with regard to grade 6 between taxa ($p > 0.1$) or when lower molars and species were grouped together ($p > 0.2$).

Protostylid, lower molars (Table 3)

According to the description made by Scott and Turner [3], the protostylid is a paramolar cusp that occurs on the buccal surface of lower molars. It is frequently associated with the



Fig. 2 ASUDAS reference plaque, hypoconulid, lower molars [3–5] and grade 6 (this study). Scoring: grade 0 (absence) to 5 (very large cusp); Grade 6 (mirror image of KB 5223, uncertain attribution, LM1): cusp 5 is larger than the hypoconid and/or the entoconid. Occlusal views. Scale bar = 1 cm / *Plaque de référence ASUDAS pour le caractère hypoconulide sur les molaires inférieures [3–5] et stade 6 (cette étude). Codage : 0 (absence) à 5 (très large cuspid) ; Stade 6 (image en miroir de KB 5223, attribution incertaine, LM1) : l’hypoconulide est plus large que l’hypoconide et/ou l’entoconide. Vues occlusales. Echelle = 1 cm*

buccal groove separating cusps 1 (protoconid) and 3 (hypoconid) and the buccal surface of cusp 1. However, a more recent study [7] showed that in Plio-Pleistocene hominins, the types of expression of this character were more similar to the development of a cingular remnant than to that of a cusp. Hlusko shows that in early hominins, the protostylid is more closely linked to the buccal groove than in modern humans and develops parallel to the occlusal surface. In our sample, almost half (48 %) of lower molars have a developed enamel crest or a large bulge centrally located on the buccal surface, extending onto both the mesial and distal cusps and almost parallel to the occlusal surface, but no apex development. When these descriptions and scoring procedures are applied [3–7], it appears that the types of expression described by Hlusko are more accurate for our sample. Our study thus confirms the readjustment of the scoring procedure that

Hlusko proposed for the protostylid [7] for Plio-Pleistocene hominins. Indeed, one specimen, at least, can be associated with each grade she proposed, unlike Scott and Turner's grades. Our proposal is to incorporate some of her newly described developmental stages in the ASUDAS protostylid reference and to assign a "model specimen" to each grade described (Fig. 3).

The following four stages are described in addition to the reference plaque:

- 4A (similar to Hlusko's grade 2): V-cleft centrally located on the buccal groove. The bottom of the groove is covered with enamel;
- 4B (similar to Hlusko's grade 3): Robust cingulum centrally located on the buccal groove with no detached apex but a cusplet frequently observed;

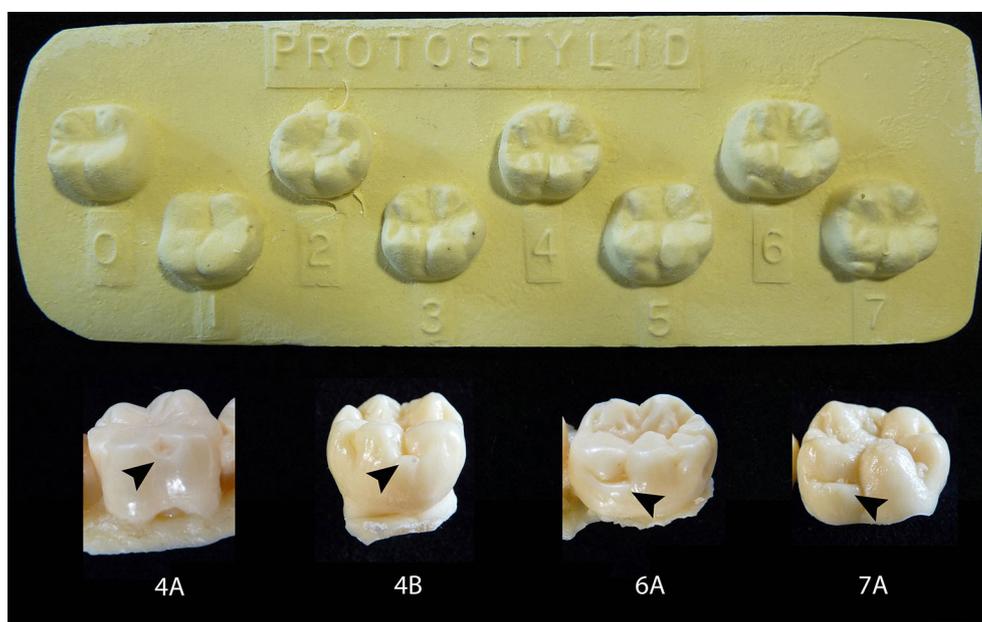


Fig. 3 New reference plaque of protostylid expression in Plio-Pleistocene hominins. ASUDAS reference plaque ([3–5]; occlusal view) and additional grades (this study and [7]; buccal views). Scoring: 4A. V-cleft centrally located on the buccal groove. The bottom of the groove is covered with enamel (mirror image of AL 333w-1b, *Au. afarensis*, RM1); 4B. Robust cingulum centrally located on the buccal groove with no apex detached but a cusplet is frequently observed (mirror image of SK 3974, *P. robustus*, RM1); 6A. Deep linear cleft is almost parallel to the occlusal surface and extends mainly onto the protoconid. The bottom of the buccal groove is covered with enamel (SK 1587a, *P. robustus*, LM2); 7A. Deep linear cleft extends onto the mesial border of the protoconid and is buccally expanded. It is almost parallel to the occlusal surface and does not show a free apex as described for the maximum grade in modern humans (MLD 2, *Au. africanus*, LM2). Scale bar = 5 mm / Développement du caractère protostylide sur les molaires inférieures chez les hominines plio-pléistocènes. Plaque de référence ASUDAS ([3–5] ; vue occlusale) et stades supplémentaires (cette étude et [7] ; vues vestibulaires). Codage : 4A. Fissure "en V" centrée sur le sillon vestibulaire. Le bas du sillon est recouvert d'émail (image en miroir de AL 333w-1b, *Au. afarensis*, RM1) ; 4B. Cingulum robuste centré sur le sillon vestibulaire sans apex mais fréquemment associé à des cuspettes accessoires (image en miroir de SK 3974, *P. robustus*, RM1) ; 6A. Fissure linéaire profonde plutôt parallèle à la surface occlusale et principalement étendue sur le protoconide. Le bas du sillon vestibulaire est recouvert (SK 1587a, *P. robustus*, LM2) ; 7A. Fissure linéaire profonde étendue sur le bord mésial du protoconide et projetée vestibulairement. La fissure est plutôt parallèle à la surface occlusale et ne présente pas d'apex libre tel qu'observé sur les hommes modernes (MLD 2, *Au. africanus*, LM2). Echelle = 5 mm

- 6A (similar to Hlusko's grade 4): Deep linear cleft is almost parallel to the occlusal surface and extends mainly onto the protoconid. The bottom of the buccal groove is covered with enamel;
- 7A (similar to Hlusko's grade 5): Deep linear cleft extending to the mesial border of the protoconid and buccally expanded. It is almost parallel to the occlusal surface and does not have a free apex as described for the maximum grade in modern humans.

See Table 7 for details of frequencies for each grade and species. Note that grade 4A is mainly observed on *P. robustus* (5/9 M₁ and 1/10 M₂) and is also scored on 1/5 *Au. africanus* M₁, 1/3 *P. boisei* M₁, 1/4 early *Homo* M₁ and 2/3 *Au. afarensis* M₂. Grade 4B is also mainly observed on *P. robustus* (2/9 M₁ and 2/10 M₂) and is scored on 1/2 *P. aethiopicus* M₂, but it is not observed on other species. Grade 6A is also mainly scored on *P. robustus* specimens (6/10 M₁ and 1/9 M₂) and on 1/3 *P. boisei* M₁ and 1/5 *Au. africanus* M₁. It is not observed on *Au. afarensis* and early *Homo* molars. Grade 7A seems more randomly distributed: it is observed on 1/5 *Au. afarensis* M₁, 1/5 *Au. africanus* M₁ and 1/1 M₂, 1/9 *P. robustus* M₁ and 1/2 *P. aethiopicus* M₂. It is not observed on early *Homo* molars.

Fisher exact tests did not reveal any significant differences between taxa on all lower molars graded 4A ($p>0.7$), 4B ($p>0.1$), 6A ($p>0.07$) or 7A ($p>0.2$).

Incorporation of supplementary morphological dental characters

Six morphological characters that are not included in ASUDAS and their types of expression are described (Table 2). An accessory distal cusp on molars had already been described and used for scoring in Bailey and Wood's study [6] as "double cusp 6" on lower molars and "cusp 6" on upper molars.

Disto-buccal cusplet, upper premolars (Table 4); Disto-buccal cusplet, lower premolars (Table 5)

As ASUDAS scores the number of lingual cusps on lower premolars [3–5], we propose to take the possible expression of a secondary buccal cusp into account, on both upper and lower premolars. In his thesis, Suwa described and scored the "development of a disto-buccal cusplet" on second upper premolars [14], but this character can be observed on

Table 4 List of constant additional characters described in the literature [2,10–12] / <i>Liste des caractères supplémentaires constants décrits dans la littérature [2,10–12]</i>
<i>Upper premolars</i>
Essential crest [11] Presence and shape of the essential crest scored on both buccal and lingual cusps Grades: 0 (absence), 1 (single crest), 2 (bifurcating crest)
Secondary ridges [12] Presence of secondary mesial and/or distal ridges on the buccal cusp Grades: 0 (absence), 1 (truncated ridge), 2 (continuous but barely discernable ridge), 3 (thin continuous ridge), 4 (medium-sized continuous ridge), 5 (thick continuous ridge)
<i>Lower premolars</i>
Transverse crest [10,11] Presence and shape of a ridge connecting the buccal and lingual cusps Grades: 0 (absence), 1 (interrupted crest), 2 (moderate expression), 3 (marked expression)
Mesiolingual groove [11] Presence of a groove on the mesiolingual aspect of the tooth Grades: 0 (absence), 1 (presence)
Metaconid placement [10,11] Position of the metaconid relative to the protoconid Grades: 1 (mesial), 2 (medial), 3 (distal)
Crown asymmetry [10,11] Shape of the lingual contour of the tooth in occlusal view Grades: 0 (symmetrical), 1 (asymmetrical), 2 (very asymmetrical)
<i>Upper molars</i>
Crista obliqua [2] Presence and shape of a crest connecting the protocone and metacone Grades: 0 (absence), 1 (continuous crest)

Table 5 List of additional dental characters described in the literature and observed in particular on Plio-Pleistocene hominins [6,14] / <i>Liste des caractères dentaires additionnels décrits dans la littérature et particulièrement observés chez les hominines plio-pléistocènes [6,14]</i>
<i>Upper premolars</i>
Disto-buccal cusplet [14] Presence of a secondary buccal cusp detached from the main buccal cusp Grades: 0 (absence), 1 (marked groove on the disto-buccal surface but no or minimal projection), 2 (disto-buccal cusplet with a free apex)
<i>Upper molars</i>
Double cusp 5 [6] Presence of a secondary distal cusp, in addition to cusp 5 [6]. Scored only if cusp 5 is also present Grades: 0 (absence), 1 (presence)
<i>Lower molars</i>
Double cusp 6 [6] Presence of a secondary distal cusp between cusps 5 and 6 [6] Grades: 0 (absence), 1 (presence)

both first and second upper and lower premolars. A large proportion of upper and lower premolars (40 % and 13 %, respectively) in our sample have a single buccal cusp. However, we observed that a buccal occlusal projection is present on several premolars on the distal side, which in some respects can be considered as an apex because it is detached from the main buccal cusp. Some premolars have a groove on the buccal surface between the main and secondary cusps. This groove is marked but the secondary cusp does not seem to be detached from the main one. Thus, as proposed by Suwa, the expression of a disto-buccal cusplet on second upper premolars [14] can be described by three grades for all the premolars. These two characters on both upper premolars (Fig. 4) and lower premolars (Fig. 5) are scored as follows:

- 0: No disto-buccal cusplet;
- 1: Marked groove on the disto-buccal surface but no or minimal projection;
- 2: Disto-buccal cusplet with a free apex.

Our results show that this character is mainly scored as present on *P. robustus* upper and lower premolars (Table 7). Grade 2 is observed on 3/6 *P. robustus* P³ and 6/7 P⁴, and on 2/4 P₃ and 7/8 P₄.

It is also frequently observed on *P. aethiopicus* (1/1 P³, 3/4 P₃, and 3/3 P₄). It is much less common in other taxa and more frequent on lower premolars. No *Homo* specimens express a grade 2 on upper premolars (0/2 P³ and 0/1 P⁴), and only 2/7 on lower premolars (1/4 P₃ and 1/3 P₄). Concerning *Au. afarensis*, the frequencies for a disto-buccal cusplet scored as grade 2 are 0/10 on P³ and P⁴, 1/2 P₃ and 2/4 P₄. It is observed on 1/4 *Au. africanus* P³ and 1/2 P₃.

Grades 0 and 1 seem more randomly distributed, but note that 2/3 P³ *Au. africanus* and 5/7 P⁴ are scored as grade 0 whereas it seems less common on other taxa (Table 4).

With regard to grade 0 and grade 2 on upper premolars, we found a significant difference between *Australopithecus* and *Paranthropus* ($p=0.02$ and $p=0.0005$, respectively). No significant differences appeared for grade 1 on upper premolars ($p>0.4$). On lower premolars, Fisher exact tests revealed significant differences between *Paranthropus* and early *Homo* for grades 0 and 2 ($p=0.006$ and $p=0.01$, respectively), but not for grade 1 ($p>0.6$).



Fig. 4 Disto-buccal cusplet, upper premolars [14]. Scoring: 1. Marked groove on the disto-buccal surface but no or minimal projection (B7–39A, *Au. aff. afarensis*, LP3); 2. Disto-buccal cusplet with a free apex (SK 824, *P. robustus*, LP4). Buccal views. Scale bar = 5 mm / *Cuspide disto-vestibulaire sur les prémolaires supérieures [14]. Codage : 1. Sillon marqué sur la surface vestibulaire mais pas d'apex libre (B7–39A, Au. aff. afarensis, LP3) ; 2. Cuspide disto-vestibulaire avec apex libre (SK 824, P. robustus, LP4). Vues vestibulaires. Echelle = 5 mm*

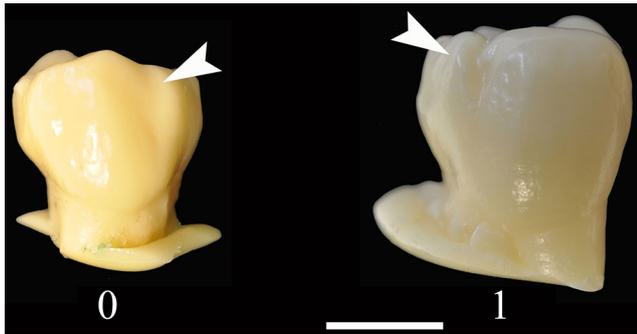


Fig. 5 Disto-buccal cusplet, lower premolars. Scoring: 1. Marked groove on the disto-buccal surface but no or minimal projection (TM 1523, *Au. africanus*, LP4); 2. Disto-buccal cusplet with a free apex (SK 7, *P. robustus*, RP4). Buccal views. Scale bar = 5 mm / *Cuspide disto-vestibulaire sur les prémolaires inférieures*. Codage : 1. Sillon marqué sur la surface vestibulaire mais pas d'apex libre (TM 1523, *Au. africanus*, LP4); 2. Cuspide disto-vestibulaire avec apex libre (SK 7, *P. robustus*, RP4). Vues vestibulaires. Echelle = 5 mm

Double cusp 5, upper molars (Table 4)

“Cusp 6” on upper molars had already been described and used for scoring in Bailey and Wood’s study [6]. To avoid confusion, we prefer to use the term “double cusp 5” on upper molars rather than “cusp 6”, which is described on lower molars. Our study provides statistical comparisons of trait frequencies between taxa, and also shows that some hominin upper molars have a small distal cusp, in addition to cusp 5. As proposed by Bailey and Wood, we scored the expression of this character on upper molars as absent (grade 0) or present (grade 1) (Fig. 6). Double cusp 5 is scored as present on 2/6 *P. robustus* M¹ and 1/6 M². Grade 1 is also

observed on 1/5 *Au. afarensis* M¹ and 1/6 early *Homo* M¹. Except for *P. robustus* specimens, it is not observed on any other taxa M²s (Table 7).

We did not find any significant differences between taxa for this character ($p > 0.3$).

Distal fovea, upper molars (Table 5)

On a large proportion of upper molars, a triangular fossa is present on the occlusal surface and distally to the metacone



Fig. 6 Occurrence of a secondary distal cusp on upper molars [6]. Scoring: 1. Presence (SK 832, *P. robustus*, LM1). Occlusal view. Scale bar = 5 mm / *Présence d'une cuspide accessoire distale sur les molaires supérieures* [6]. Scoring: 1. Présence (SK 832, *P. robustus*, LM1). Vue occlusale. Echelle = 5 mm

Table 6 List of new non-metric dental characters described in this study / <i>Liste des nouveaux caractères dentaires proposés dans cette étude</i>
<i>Lower premolars</i>
Disto-buccal cusplet Presence of a secondary buccal cusp detached from the main buccal cusp Grades: 0 (absence), 1 (marked groove on the disto-buccal surface but no or minimal projection), 2 (disto-buccal cusplet with a free apex)
<i>Upper molars</i>
Distal fovea Development of a triangular depression mesial to the distal marginal ridge Grades: 0 (absence), 1 (small distal fovea), 2 (large distal fovea. Distal crests on hypocone and metacone converge to form a large fovea which extends almost to the summits of distal cusps)
<i>Lower molars</i>
Mesial marginal ridge Development of the mesial marginal ridge Grades: 0 (absence), 1 (ridge is continuous and thin), 2 (ridge is uninterrupted, thick and sometimes closes the anterior fovea)

Table 7 Trait frequencies for each character for all groups / *Distributions des fréquences de chaque caractère pour chacun des groupes*

		<i>Au.</i> <i>afarensis</i>	<i>Au.</i> <i>africanus</i>	<i>Au.</i> <i>bahrelghazali</i>	<i>P.</i> <i>aethiopicus</i>	<i>P. boisei</i>	<i>P. robustus</i>	<i>Early</i> <i>Homo</i>	<i>H.</i> <i>georgicus</i>
Maxilla									
P ³ Disto- buccal cusplet	0	2/3	1/4	–	0/1	–	1/6	1/2	–
	1	1/3	2/4	–	0/1	–	2/6	1/2	–
	2	0/3	1/4	–	1/1	–	3/6	0/2	–
P ⁴ Disto- buccal cusplet	0	5/7	1/1	–	–	–	1/7	1/1	–
	1	2/7	0/1	–	–	–	0/7	0/1	–
	2	0/7	0/1	–	–	–	6/7	0/1	–
M ¹ Hypocone	3	0/5	0/4	–	0/1	0/1	0/6	0/6	–
	4	1/5	0/4	–	0/1	0/1	0/6	0/6	–
	5	3/5	3/4	–	0/1	0/1	3/6	4/6	–
	6	1/5	1/4	–	1/1	1/1	3/6	2/6	–
M ¹ Double Cusp 5	0	4/5	4/4	–	1/1	0/1	4/6	5/6	–
	1	1/5	0/4	–	0/1	1/1	2/6	1/6	–
M ¹ Distal Fovea	0	1/5	0/4	–	0/1	1/1	0/6	0/6	–
	1	4/5	2/4	–	1/1	0/1	6/6	1/6	–
	2	0/5	2/4	–	0/1	0/1	0/6	5/6	–
M ² Hypocone	3	0/2	0/2	–	–	–	0/6	1/4	–
	4	0/2	0/2	–	–	–	0/6	0/4	–
	5	1/2	0/2	–	–	–	2/6	3/4	–
	6	1/2	2/2	–	–	–	4/6	0/4	–
M ² Double Cusp 5	0	2/2	2/2	–	–	–	5/6	4/4	–
	1	0/2	0/2	–	–	–	1/6	0/4	–
M ² Distal Fovea	0	1/2	0/2	–	–	–	1/6	0/4	–
	1	1/2	2/2	–	–	–	4/6	2/4	–
	2	0/2	0/2	–	–	–	1/6	2/4	–
Mandible									
P ₃ Disto- buccal cusplet	0	0/2	0/2	0/1	0/4	–	0/4	1/4	1/1
	1	1/2	1/2	0/1	1/4	–	2/4	2/4	0/1
	2	1/2	1/2	1/1	3/4	–	2/4	1/4	0/1
P ₄ Disto- buccal cusplet	0	1/4	–	0/1	0/3	–	0/8	1/3	1/1
	1	1/4	–	0/1	0/3	–	1/8	1/3	0/1
	2	2/4	–	1/1	3/3	–	7/8	1/3	0/1
M ₁ Hypoconulid	3	0/5	0/5	–	0/1	1/3	0/11	0/4	0/1
	4	0/5	0/5	–	0/1	0/3	3/11	1/4	0/1
	5	5/5	5/5	–	1/1	0/3	6/11	3/4	1/1
	6	0/5	0/5	–	0/1	2/3	2/11	0/4	0/1

(Suite page suivante)

Table 7 (suite)										
		<i>Au. afarensis</i>	<i>Au. africanus</i>	<i>Au. bahrelghazali</i>	<i>P. aethiopicus</i>	<i>P. boisei</i>	<i>P. robustus</i>	<i>Early Homo</i>	<i>H. georgicus</i>	
M ₁ Protostylid	0	0/5	2/5	–	0/1	1/3	0/9	2/4	0/1	
	1	0/5	0/5	–	0/1	0/3	0/9	0/4	0/1	
	2	0/5	0/5	–	0/1	0/3	0/9	0/4	0/1	
	3	0/5	0/5	–	0/1	0/3	0/9	0/4	0/1	
	4	4/5	0/5	–	0/1	0/3	0/9	0/4	0/1	
	4A	0/5	1/5	–	0/1	1/3	5/9	1/4	0/1	
	4B	0/5	0/5	–	0/1	0/3	2/9	0/4	0/1	
	5	0/5	0/5	–	0/1	0/3	0/9	0/4	0/1	
	6	0/5	0/5	–	1/1	0/3	0/9	1/4	1/1	
	6A	0/5	1/5	–	0/1	1/3	1/9	0/4	0/1	
M ₁ Double Cusp 6	0	4/4	4/5	–	1/1	1/3	10/11	5/5	1/1	
	1	0/4	1/5	–	0/1	2/3	1/11	0/5	0/1	
	M ₁ Mesial Marginal Ridge	0	0/5	1/5	–	0/1	0/3	0/7	1/4	1/1
		1	3/5	1/5	–	1/1	0/3	2/7	1/4	0/1
	M ₂ Hypoconulid	2	2/5	3/5	–	0/1	3/3	5/7	2/4	0/1
		3	0/3	0/1	–	0/3	–	0/9	0/4	0/1
		4	2/3	0/1	–	1/3	–	4/9	2/4	0/1
		5	0/3	1/1	–	1/3	–	4/9	2/4	1/1
	M ₂ Protostylid	6	1/3	0/1	–	1/3	–	1/9	0/4	0/1
		0	0/3	0/1	–	0/2	–	0/10	4/4	0/1
1		0/3	0/1	–	0/2	–	0/10	0/4	0/1	
2		0/3	0/1	–	0/2	–	0/10	0/4	0/1	
3		0/3	0/1	–	0/2	–	0/10	0/4	0/1	
4		0/3	0/1	–	0/2	–	0/10	0/4	0/1	
4A		2/3	0/1	–	0/2	–	1/10	0/4	1/1	
4B		0/3	0/1	–	1/2	–	2/10	0/4	0/1	
5		1/3	0/1	–	0/2	–	0/10	0/4	0/1	
6		0/3	0/1	–	0/2	–	1/10	0/4	0/1	
M ₂ Double Cusp 6	6A	0/3	0/1	–	0/2	–	6/10	0/4	0/1	
	7	0/3	0/1	–	0/2	–	0/10	0/4	0/1	
	7A	0/3	1/1	–	1/2	–	0/10	0/4	0/1	
	0	3/3	1/1	–	2/3	–	5/9	4/4	1/1	
	1	0/3	0/1	–	1/3	–	4/9	0/4	0/1	
	M ₂ Mesial Marginal Ridge	0	0/3	0/1	–	0/2	–	0/9	0/4	1/1
		1	1/3	0/1	–	0/2	–	1/9	2/4	0/1
		2	2/3	1/1	–	2/2	–	8/9	2/4	0/1

and the hypocone. We propose scoring the expression of the distal fovea on upper molars as follows (Fig. 7):

- 0: Absence, or very slight development;
- 1: Small distal fovea;
- 2: Large distal fovea, distal crests of distal cusps converging to form a large fossa that extends almost to the summit of the distal cusps.

The distal fovea seems to be well developed on the majority of early *Homo* (5/6 M¹ and 2/4 M² scored as grade 2). *P. robustus* specimens mainly express a grade 1: 6/6 M¹ and 4/6 M². We scored the distal fovea as grade 1 on 2/4 *Au. africanus* M¹ and 2/2 M². *Au. afarensis* specimens are only scored as grades 0 (1/5 M¹ and 1/2 M²) and 1 (4/5 M¹ and 1/2 M²). The single *P. boisei* specimen (M¹) is scored as grade 0 and the single *P. aethiopicus* specimen (M¹) as grade 1 (Table 7).

Fisher exact tests revealed significant differences in grade 2 between *Australopithecus* and early *Homo* ($p=0.01$) and between *Paranthropus* and early *Homo* ($p=0.002$). For grade 1, we found a significant difference only between *Paranthropus* and early *Homo* ($p=0.02$). No significant differences appeared for grade 0 ($p>0.5$).

Double cusp 6, lower molars (Table 4)

A small secondary distal cusp located between cusps 5 and 6 is often observed on several lower molars. This character had already been described as “double cusp 6” in several studies [6,15,16]. Bailey and Wood’s study on occlusal morphology points out that it is useful for distinguishing between taxa or assessing phenetic relationships [6]. Our study provides statistical comparisons of trait frequencies between taxa. This character was scored only if cusps 5 and 6 were present, so that a distinction could be made

between these cusps instead of scoring the same cusp twice. As proposed by Bailey and Wood, we scored this character as absent (grade 0) or present (grade 1) (Fig. 8).

This character is observed mostly on *P. robustus* specimens (Table 7). It is observed on 4/9 M₂ but only 1/11 M₁. Concerning *P. boisei* specimens, 2/3 M₁ have a double cusp 6. It is only observed on 1/5 *Au. africanus* M₁ and not on M₂. It is not observed on any *Au. afarensis* (0/4 M₁ and 0/3 M₂) or early *Homo* (0/5 M₁ and 0/4 M₂). There is no significant difference between groups with regard to the presence or absence of double cusp 6 ($p>0.08$).

Mesial marginal ridge, lower molars (Table 5)

In our sample, Plio-Pleistocene hominin lower molars have different types of expression of the mesial marginal ridge, which is absent on some molars but can also be more or less developed. In a few cases, we observed a thick marginal ridge that obliterates the anterior fovea.

We propose the following scoring procedure for the expression of this character (Fig. 9):

- 0: Mesial marginal ridge absent or very slight;
- 1: Mesial marginal ridge is continuous and thin;
- 2: Mesial marginal ridge is continuous, thick and can sometimes close the anterior fovea.

A mesial marginal ridge (grades 1 and 2) is frequently observed on Plio-Pleistocene molars ($n=42$). In our sample, it was absent only on two M₁, and never absent on M₂ (Table 7). We scored this character as grade 2 on 5/7 *P. robustus* M₁ and 8/9 M₂. 2/4 early *Homo* M₁ and 2/4 M₂ express a grade 2. The three *P. boisei* molars (M₁) express a grade 2. The frequencies for grades 1 are 3/5 M₁ and 1/3 M₂ for *Au. afarensis*, and 1/5 M₁ for early *Homo*. The

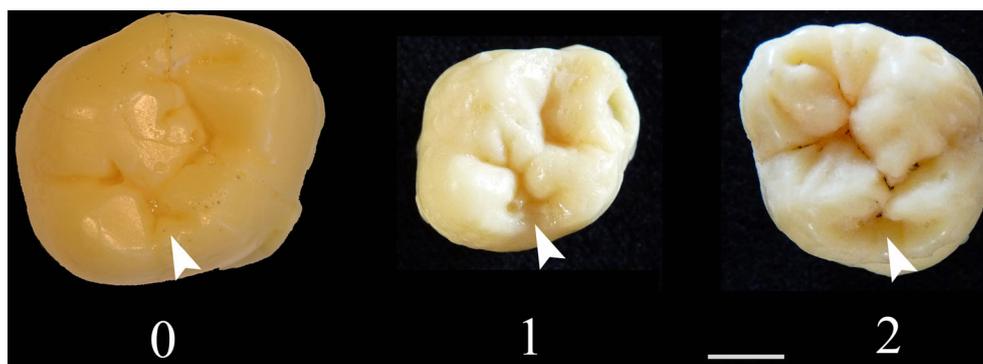


Fig. 7 Distal fovea, upper molars. Scoring: 0. Absence or very slight development (SK 835, *P. robustus*, LM2); 1. Small distal fovea (B8-23B, *Au. aff. afarensis*, LM1); 2. Large distal fovea, distal crests of distal cusps converging to form a large fossa which extends almost to the summits of distal cusps (KB 5223, uncertain attribution, RM2). Occlusal views. Scale bar = 5 mm / Fosse distale sur les molaires supérieures. Codage : 0. Absence ou très faible développement (SK 835, *P. robustus*, LM2) ; 1. Petite fosse distale (B8-23B, *Au. aff. afarensis*, LM1) ; 2. Large fosse distale. Les crêtes distales des cuspidés distales se rejoignent à distance formant une large fosse qui s’étend presque jusqu’aux sommets des cuspidés distales (KB 5223, attribution incertaine, RM2). Vues occlusales. Echelle = 5 mm

frequencies for grade 2 are 2/5 M_1 and 2/3 M_2 for *Au. afar-ensis* and 3/5 M_1 and 1/1 M_2 for early *Homo*. We found significant differences between *Paranthropus* and early *Homo* for grades 0 ($p=0.02$) and 2 ($p=0.04$), but not for grade 1 ($p>0.2$).

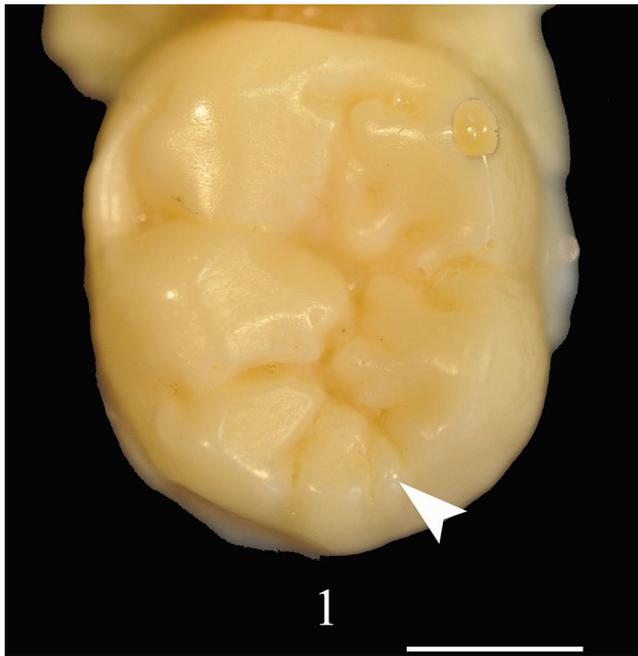


Fig. 8 Occurrence of a secondary distal cusp on lower molars [6]. Scoring: 1. Presence (SK 1587a, *P. robustus*, LM2). Occlusal view. Scale bar = 5 mm / Présence d'une cuspide accessoire distale sur les molaires inférieures [6]. Scoring: 1. Présence (SK 1587a, *P. robustus*, LM2). Vue occlusale. Echelle = 5 mm

Conclusion

Our study based on observations and scoring of 178 premolars and molars demonstrates that the standard scoring system for dental morphological characters (ASUDAS) does not cover all morphological variations in Plio-Pleistocene hominins. The purpose of this note is to emphasize the need to develop standard scoring for these characters, which are useful to assess variations in premolars and molars in fossil hominins. We propose to readjust this standard scoring system by, firstly, adding grades for the types of expression of dental characters already described, and secondly, by including the new types of expression described by Hlusko [7] on the protostylid reference plaque, and finally by describing six characters that are not included in the standard system.

Firstly, our observations suggest that there is a size parameter that creates a bias in the scoring procedure for some characters. This is because ASUDAS was established for the study of modern human teeth, which are smaller than those of extinct hominins. Therefore, in order to score every molar in our sample accurately, we suggest adding a sixth grade for two characters: the hypocone on upper molars and the hypoconulid on lower molars. We propose a description based on the size of the cusp relatively to the adjacent cusp, in order to limit the bias arising from the size parameter.

Furthermore, our study confirms the new scoring procedure developed by Hlusko for the protostylid on lower molars [7]. According to Hlusko, the expression of this character in *Australopithecus* is more similar to that of a cingular remnant than to that of a cusp as initially described in ASUDAS for modern humans. Our observations re-confirm that

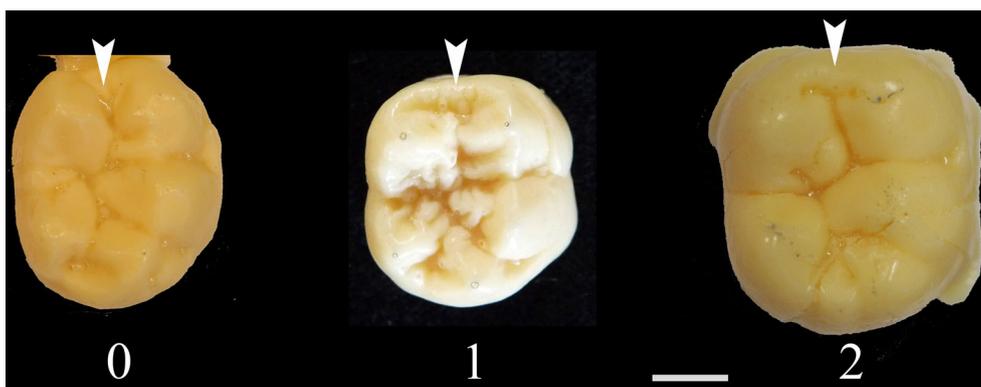


Fig. 9 Types of expression of the mesial marginal ridge, lower molars. Scoring: 0. Mesial marginal ridge absent or very slight (Stw 151, *Au. africanus*, RM1); 1. Ridge is continuous and thin (W7-508, *Au. aff. afarensis*, RM1); 2. Ridge is continuous, thick, and can obliterate the anterior fovea (SKW 4767, *P. robustus*, RM1). Occlusal views. Scale bar = 5 mm / Développement de la crête marginale mésiale sur les molaires inférieures. Codage : 0. Absence ou faible développement (Stw 151, *Au. africanus*, RM1) ; 1. Crête continue et fine (W7-508, *Au. aff. afarensis*, RM1) ; 2. Crête continue et robuste, pouvant combler la fosse antérieure (SKW 4767, *P. robustus*, RM1). Vues occlusales. Echelle = 5 mm

the types of expression described by Hlusko should be illustrated in the standard system to allow accurate and standardized scoring for Plio-Pleistocene hominins.

Our study describes six characters that are not included in the standard ASUDAS [3–5]. A secondary distal cusp on upper and lower molars has already been described [6] and our observations also suggest that it may have the potential to establish distinctions between taxa. We believe that the disto-lingual cusplet on second upper premolars described by Suwa [14] can be recorded on both first and second upper and lower premolars. However, our results suggest that it is useful for distinguishing *P. robustus* upper premolars, but that it is more randomly distributed on lower premolars. We have kept a basic present/absent description for double cusp 5 on upper molars and double cusp 6. However, we stress the need to propose more accurate scoring procedures that are not based solely on the occurrence (or not) of the character.

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