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Early *Homo* at Kromdraai B: probabilistic and morphological analysis of the lower dentition

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Abstract

Kromdraai B, situated less than 2 km east of Sterkfontein, in the Gauteng province of South Africa, has yielded 27 specimens, attributed to a single Plio-Pleistocene hominid species, including the type specimen of *Paranthropus (Australopithecus) robustus*. By using resampling and morphological analysis, and after considering the most diagnostic features that have been used in the past for the lower dentition, we here suggest that one specimen from Kromdraai B, KB 5223, is clearly distinct from *P. robustus* and represents early *Homo*. **To cite this article:** J. Braga, J.F. Thackeray, C. R. Palevol 2 (2003).

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Résumé

« Early *Homo* » à Kromdraai B : analyses probabiliste et morphologique de la denture mandibulaire. Le site de Kromdraai B, situé à moins de 2 km à l'est de Sterkfontein, dans la province du Gauteng (Afrique du Sud), a livré 27 restes, dont l'holotype, d'une espèce d'hominidé fossile du Plio-Pléistocène : *Paranthropus (Australopithecus) robustus*. Après avoir réalisé une analyse probabiliste et morphologique, nous proposons ici l'attribution de l'un de ces fossiles de Kromdraai B, KB 5223, aux premiers représentants du genre *Homo*. Pour ce faire, nous utilisons les caractères dentaires les plus diagnostiques utilisés jusqu'ici pour distinguer les premiers représentants du genre *Homo* à la fois de *Paranthropus (Australopithecus) robustus/boisei* et de *Australopithecus africanus*. **Pour citer cet article :** J. Braga, J.F. Thackeray, C. R. Palevol 2 (2003).

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L'attribution taxinomique des restes d'hominidés fossiles est souvent assortie d'une incertitude, variable selon le degré de préservation. Ce problème trouve un écho particulier dans le cas des plus anciens représentants du genre *Homo* (« early *Homo* »), fossiles attribués ou affiliés à *Homo habilis* [12]. En effet, parmi eux, certains sont-ils, à tort, attribués à ce groupe ? À l'inverse, d'autres devraient-ils être rangés dans ce groupe ? Les descriptions et les analyses synthétiques [17, 20, 21], les découvertes [7, 11, 13, 16] d'hominidés fossiles d'âge Plio-Pléistocène, parfois très fragmentaires, survenues après la diagnose d'*Homo habilis*, en 1964 [12], nous conduisent à formuler ces deux questions. Par conséquent, nous examinons ici le cas des fossiles provenant du site de Kromdraai B [10, 19], en utilisant de nombreuses données non disponibles lors de leur description initiale, et en nous limitant aux dents mandibulaires. Pour ces dernières, le caractère diagnostique le plus marquant d'*Homo habilis* est une réduction du diamètre vestibulo-lingual (VL), tout particulièrement, des premières molaires permanentes (M_1). Cela induit un accroissement de l'indice mésio-distal/vestibulo-lingual (MD/VL) [7, 11–13, 17, 20, 21], mais aussi une réorganisation des cuspidés et, particulièrement, l'apparition du tuberculum intermedium (C7, sensu stricto) ou du postmétacaulide (C7, sensu lato), associée à la disparition du tuberculum sextum (C6) [7, 13, 18]. À cette morphologie, il faut ajouter : un allongement mésio-distal de la couronne des incisives permanentes [9, 12], dont l'extrémité distale du bord libre forme un angle obtus. Quant aux molaires déciduales attribuées à « early *Homo* », elles sont peu nombreuses, seule la distinction *Paranthropus/Australopithecus* étant bien documentée [6]. Aux caractères macromorphologiques, il faut ajouter des traits de la microstructure de l'émail, dont la validité taxinomique est parfois mise en doute [14] : une distribution particulière de l'épaisseur de l'émail et l'angle de la jonction dento-énamellaire [1], la distribution et le nombre de périkymaties sur la face vestibulaire des dents antérieures [3].

L'hypothèse de la présence d'« early *Homo* » Kromdraai B est ici testée par l'analyse morphologique et métrique de KB 5223, une denture mixte mandibulaire incomplète (Fig. 1), décrite par Grine [5] puis par

Kaszycka [10]. Trois échantillons représentant « early *Homo* », *Paranthropus robustus* et *P. boisei* sont utilisés à titre de comparaison (Tableau 1). Aux variables qualitatives définies par Robinson [15], nous ajoutons quatre caractères métriques pour l'importante place qu'ils occupent dans la diagnose du genre *Homo* : les diamètres MD et VL, l'indice MD/VL et l'aire de la face occlusale MD \times VL. Une procédure de ré-échantillonnage, ou *resampling* [4], avec remise, est utilisée ici. Afin de limiter le nombre des échantillons identiques, les effectifs des échantillons simulés sont inférieurs de moitié à ceux des échantillons initiaux. Dans un premier temps, afin de tester la pertinence d'une distinction quantitative claire entre, d'une part, « early *Homo* » et *P. robustus*, d'autre part, *P. robustus* et *P. boisei*, nous combinons les échantillons de comparaison. Nous tirons 500 fois au sort, avec remise, deux groupes de dents ayant alors perdu toute attribution taxinomique. Nous examinons ensuite la distribution des 500 écarts entre les moyennes calculées pour les deux groupes de dents, pour les quatre caractères, et pour chaque type de dent considérée. Si un écart supérieur à celui existant réellement entre nos deux échantillons de comparaison est observé dans au moins 5% des cas (Tableau 2), cela signifie que l'écart réel observé peut être lié au hasard et n'a, pas conséquent, aucune signification taxinomique. Après ce premier test, nous comparons les mesures de KB 5223 à des distributions simulées (après 500 tirages avec remise) représentant des échantillons de dents attribuées à *P. robustus* et « early *Homo* » (Fig. 2, pour la M_1). Si la valeur de KB 5223 est située en dehors des limites de confiance (au seuil de 95%) de la distribution ainsi générée (Fig. 2, pour la M_1), l'hypothèse nulle d'absence de différence est rejetée.

Les raisons nous conduisant à accepter l'attribution de KB 5223 à « early *Homo* » sont, tout d'abord, métriques. En effet, les caractères distinctifs d'« early *Homo* » et de *Paranthropus robustus*, dont la validité taxinomique a été préalablement testée, sont : un diamètre VL réduit et un important indice MD/VL de la M_1 ; toutes les valeurs de la dm_2 , à l'exception de l'indice MD/VL. L'étude morphologique confirme le résultat de ce test : KB 5223 présente des caractères diagnostiques du genre *Homo* (absence de C6 et présence de C7, sensu lato, sur la M_1) ou très éloignés de ceux de *Paranthropus* (absence d'hypoconulide et de cuspidé accessoire mésiale sur la dm_1 à quatre

cuspidés, absence de C6 et présence de postmétacoulide sur la dm_2 , angle obtus de l'extrémité distale du bord libre des incisives permanentes). L'analyse de la microstructure de l'émail de KB 5223 [3, 8] ne permet pas de le distinguer clairement d'early *Homo* [1, 3]. Par ailleurs, certains représentants d'early *Homo* [2] montrent des valeurs plus proches de *Paranthropus* que de KB 5223.

L'interprétation des hominidés fossiles de Kromdraai B a souvent fait l'objet de débats importants [10]. Mais cet échantillon représente-t-il une seule espèce ? Il est essentiellement composé de dents isolées, dont l'attribution taxinomique mérite d'être discutée. En effet, comme pour de nombreuses autres dents isolées d'hominidés fossiles provenant d'autres sites africains d'âge Pliocène ou Pléistocène, toute attribution taxinomique est assortie d'un degré d'incertitude restant souvent à évaluer. Pour ce faire, nous proposons ici une méthode basée sur la simulation d'échantillonnage et nous développons l'exemple de KB 5223. À la suite, à la fois de tests après simulation d'échantillons et d'une analyse morphologique, il apparaît que l'attribution de KB 5223 à *Paranthropus* est fortement contre-indiquée. Au contraire, son attribution à « early *Homo* » ne l'est pas, les caractères les plus diagnostiques de ce groupe, pour les dents mandibulaires permanentes, étant présents sur KB 5223.

1. Introduction

How can we best address difficulties associated with taxonomic sorting of fossil hominid remains? This question is important when dealing with early *Homo* material that has been allocated to, or likened to *Homo habilis*, since its naming by Leakey et al. [12]. Indeed, the distinctiveness and morphological integrity of the earliest known representatives of the genus *Homo* has generated continuous debate. Is early *Homo* an amalgamation of 'derived' and 'primitive' australopithecine-like specimens? Alternatively, have at least some early *Homo* remains been inadvertently referred to an australopithecine taxon? Morphological and morphometric surveys of Plio-Pleistocene hominid cranial remains studied by Suwa [17], Tobias [20] and Wood [21], as well as the analysis of additional specimens that have since been discovered, demonstrate how it is necessary to constantly bring up-to-date the lists of

unequivocal quantitative and qualitative criteria for the taxonomic allocation of hominid remains.

This paper concentrates on the lower dentition and tests the hypothesis that *Homo* is represented at Kromdraai B. At the time of the initial description of most hominids from Kromdraai B (see [10, 19] for a review), many dental remains now attributed to early *Homo* had not yet been discovered [7, 11, 13, 16]. Moreover, detailed descriptions of large samples of teeth were not available [17, 20, 21]. We now undertake a study, incorporating new data, with a focus on comparative statistics (resampling) that are relevant to hominid taxonomy.

Many authors regard the mandibular postcanine dentition of Plio-Pleistocene hominids as taxonomically diagnostic [18, 22], the allocations of East African fossil hominid remains being generally less controversial. A buccolingual (BL) narrowing (with buccal and lingual faces that are almost vertical), a mesiodistal (MD) elongation of the mandibular permanent molars, or a combination of both (a high MD/BL shape index), and a rearrangement of the distal cusps, are among the features often considered to be relevant to the identification of the genus *Homo* [7, 11–13, 17, 18, 20, 21]. When Tobias [20 (p. 30)] considered the major traits 'we should call today apomorphies of the *Homo* lineage', he referred to the lack of M_1 buccolingual expansion (named by him the 'australopithecine bulge'), expected to raise the MD/BL index. The BL narrowness or the high MD/BL index of M_1 has also been considered to be a strong indicator, either of early *Homo* from Swartkrans Member 2 [7], Drimolen [11] and the Omo Valley [17], or of "a hominid taxon that is more derived towards an early *Homo* condition" than other hominids from Sterkfontein Member 4 [13 (p. 462)]. The presence of a tuberculum intermedium on the M_1 , or the presence of a postmetacoulid, combined with the lack of a tuberculum sextum, has also been considered to be an indicator of early *Homo* from Swartkrans [7] and Sterkfontein [13], or "highly suggestive of a nonrobust taxon" represented by teeth from the Omo collection spanning the 3–2 million years (Myr) [18 (p. 254)]. Some features relevant to the diagnosis of the genus *Homo* have also been described on the basis of lower anterior permanent teeth. Leakey et al. [12] and Howell [9] considered that a species of the genus *Homo* are characterised by incisors relatively enlarged mesiodistally in comparison with those of

Australopithecus. Grine [7] noted the mammellate incisal edges with distal extremities strongly bevelled with an obtuse corner. The lower deciduous molars of early *Homo* are still poorly known because of the paucity of specimens from both eastern and southern Africa. Despite this fact, Grine [6] revealed a number of traits in the deciduous molars that differ in *Australopithecus* and *Paranthropus*. Ramirez-Rozzi [14] questioned the taxonomic validity of many macrostructural characteristics because of a lack of comparative data in extant hominoids. Moreover, he also expressed serious doubts about microstructural features as a taxonomic tool.

Measurements of enamel thickness and the slope of the striae of Retzius relative to the enamel-dentine junction (EDJ) have been used for taxonomic purposes. Beynon and Wood [1] found that certain values of enamel thickness (CT and OT) were significantly greater in *P. boisei* compared with East African early *Homo*. They also observed that the angle of the striae of Retzius with respect to the EDJ was lower in *P. boisei* compared with early *Homo*, indicating faster rates of crown extension during amelogenesis in the former. Dean and Reid [3] examined perikymata spacing and distribution on the buccal enamel surface of anterior teeth. They observed that the distribution of perikymata counts in *Australopithecus* and *Paranthropus* essentially follows the same trend as in modern humans, but with consistently fewer perikymata per millimetre. Some teeth attributed to *Homo erectus* and *Homo rudolfensis* resemble *Paranthropus* in their perikymata spacing and distribution, contrasting with the pattern observed in extant humans.

2. Material

To test the hypothesis that *Homo* is represented in early Pleistocene deposits at Kromdraai B, we focus attention on KB 5223, incomplete mandibular dentition from in situ Member 3 breccia of the Kromdraai B East Formation (27.04 m east, 2.6 m north, and 1.50 m below reference datum of Vrba's excavation grid). This dentition (Fig. 1), first described by Grine [5], and later by Kaszycka [10], comprises M_1 and dm_2 antimeres, all the permanent lower incisors, the left d_c , dm_1 and lower permanent canine. The right lateral lower permanent incisor was subsequently found by Delson.

Current dating indicates that early *Homo* appeared perhaps as early as 2.4 Myr, and is last recorded at about 1.6 Myr. Fossil specimens allocated to *Paranthropus boisei* and *P. robustus* span the time period from approximately 2.4 to ca 1.3 Myr. We select three broadly contemporaneous and sympatric reference samples of lower teeth (Table 1) representing early *Homo* (StW 151, DNH 35, Skx 257/258, Sk 45, SK 15, ER 806, ER 820, ER 992, ER 1482A, ER 1502, ER 1506, ER 1507, ER 1508, ER 1801, ER 1802, ER 1812, ER 3734, OH 7, OH 13, OH 16, OH 22, OH 37, UR 501, Omo 75S.1969.15, Omo 75.1969.14a), *P. robustus* (TM 1517, TM 1536, TM 1601, TM 1604, KB 5503, SK 6, SK 23, SK 25, SK 34, SK 55, SK 61, SK 62, SK 63, SK 64, SK 74, SK 104, SK 438, SK 482/869, SK 828, SK 838b, SK 839/852, SK 841, SK 842, SK 843/846a, SK 845, SK 858/861, SK 876, SK 1587, SK 1588, SK 1648, SK 3974, SK 3978, SKX 1017, SKX 1313, SKX 3559, SKX 4446, SKX 5004b, SKX 5013, SKX 5023, SKX 7992, SKX 26967, DNH 2, DNH 8, DNH 44, DNH 47, DNH 56, DNH 60, DNH 67, DNH 80), and *P. boisei* (ER 729, ER 730, ER 801, ER 1477, ER 1509, ER 1816, ER 1820, ER 3230, ER 3890, OH 30, Omo 18-34, Omo 18–40, Omo 47–45, L 64–2, L 704–2, Peninj). As a first step, we use taxonomic attributions based on macrostructural features to group teeth in their reference samples, even though no consensus has as yet been reached.

3. Methods

3.1. Qualitative analysis

Morphological assessments of KB 5223, used to confirm or refute our quantitative tests (see below), are made with reference to Robinson's odontological terminology [15]. The tuberculum sextum (C6) is a cuspid located between the hypoconulid and entoconid, in the posterior fovea. The tuberculum intermedium (C7) is a cuspid separated from the metaconid and entoconid by well-defined grooves and reaching up to the central fossa. The postmetaconulid is an elevation on the distolingual part of the metaconid, incompletely separated from it. Some authors consider that the postmetaconulid constitutes minimal C7 expression. We consider them as a C7, *sensu lato*. The mesial accessory cuspid (or mesioconulid) is an accessory cuspid located along the mesial marginal ridge, mesial

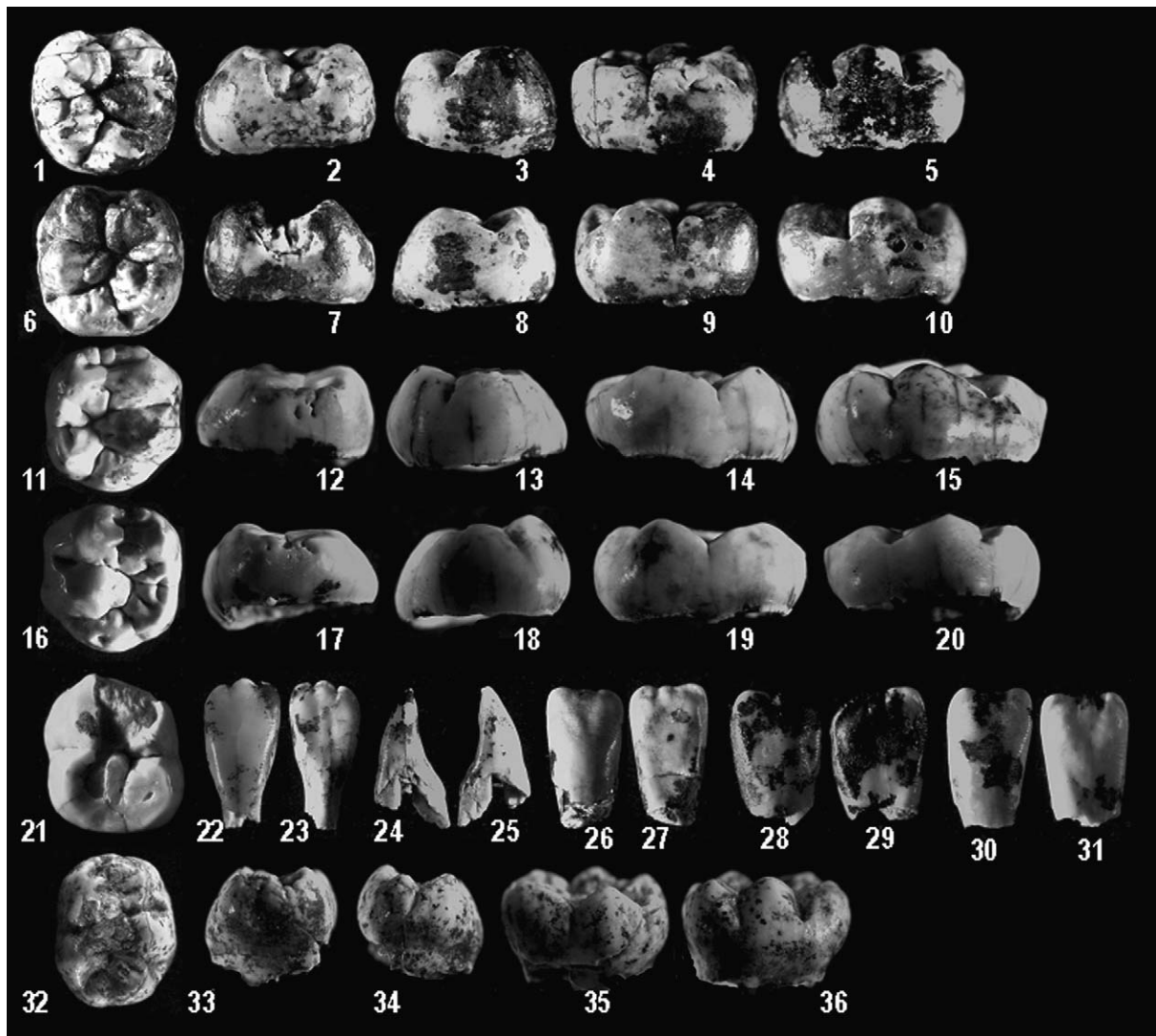


Fig. 1. From left to right and from top to bottom: KB 5223 (views 1 to 31) and KB 5503 (views 32 to 36). KB 5223: views 1 to 5, right M₁, occlusal (1), mesial (2), distal (3), lingual (4) and buccal (5). Views 6 to 10, left M₁, occlusal (6), mesial (7), distal (8), lingual (9) and buccal (10). Views 11 to 15, right dm₂, occlusal (11), mesial (12), distal (13), lingual (14) and buccal (15). Views 16 to 20, left dm₂, occlusal (16), mesial (17), distal (18), lingual (19) and buccal (20). 21, Left dm₁, occlusal view. Views 22 to 25, right I₂, buccal (22), lingual (23), mesial (24) and lateral. Views 26 and 27, left I₁, buccal (26), lingual (27). Views 28 and 29, left I₂, buccal (28), lingual (29). Views 30 and 31, right I₁, buccal (30), lingual (31). KB 5503: views 32 to 36, right dm₂, occlusal (32), mesial (33), distal (34), lingual (35) and buccal (36).

Fig. 1. De gauche à droite et de haut en bas : KB 5223 (vues 1 à 31) et KB 5503 (vues 32 à 36). KB 5223, vues 1 à 5, M₁ droite, occlusale (1), mésiale (2), distale (3), linguale (4) et vestibulaire (5). Vues 6 à 10, M₁ gauche, occlusale (6), mésiale (7), distale (8), linguale (9) et vestibulaire (10). Vues 11 à 15, dm₂ droite, occlusale (11), mésiale (12), distale (13), linguale (14) et vestibulaire (15). Vues 16 à 20, dm₂ gauche, occlusale (16), mésiale (17), distale (18), linguale (19) et vestibulaire (20). 21, dm₁ gauche, vue occlusale. Vues 22 à 25, I₂ droite, vestibulaire (22), linguale (23), mésiale (24) et latérale. Vues 26 et 27, I₁ gauche, vestibulaire (26), linguale (27). Vues 28 et 29, I₂ gauche, vestibulaire (28), linguale (29). Vues 30 et 31, I₁ droite, vestibulaire (30), linguale (31). KB 5503 : vues 32 à 36, dm₂ droite, occlusale (32), mésiale (33), distale (34), linguale (35) et vestibulaire (36).

to the protoconid. The mesial marginal ridge is a crest delineating the mesial edge of the occlusal surface. The

trigonid crest bridges both mesial cusps. The postenocristid is a crest connecting the entoconid and the hypo-

Table 1

Mandibular permanent teeth samples of the present study.

Tableau 1. Échantillons des dents permanentes mandibulaires étudiées ici.

	M1	dm2	dm1	I2	I1
Early <i>Homo</i>	32	7	6	5	4
<i>Paranthropus robustus</i>	33	22	14	9	11
<i>Paranthropus boisei</i>	13	4	3	8	11
KB 5223	2	2	1	1	2

conulid and delineates anteriorly the posterior fovea. The distal marginal ridge delineates the distal edge of the occlusal surface. The anterior fovea (trigonid basin) is a depressed area located between the mesial marginal ridge and the trigonid crest. The posterior fovea is a depressed area bounded by the distal marginal ridge and the postenocristid.

3.2. Quantitative analysis

Four quantitative traits are used: the MD and BL crown diameters (in mm), mainly from published accounts (mainly from references 4 and 7), as well as the calculated MD/BL index and occlusal area (MD × BL). The analysis of the small data sets available so far (Table 1) is done by a two-step resampling procedure, with replacement. In both steps, to reduce the effect of similarity (due to replacement) between hypothetical samples, their size is determined by half the number of fossil teeth available for each category (Tables 1 and 2). Contrary to traditional parametric tests, resampling does not require making restrictive assumptions (like randomly sampling from normally distributed popula-

tions with equal variances) about the underlying distributions of the qualitative traits [4]. Indeed, when dealing with small datasets, the validity of the assumptions made to use traditional parametric tests should be properly confirmed. If not, the results of such test are meaningless.

The preliminary step of our quantitative testing of the presence of early *Homo* at Kromdraai B is not based on previous taxonomic attributions. We initially combine reference samples and assume that they represent one taxonomic group. The null hypothesis is that there is no difference between samples. If we conclude that the observed difference between two samples under consideration is unlikely to have occurred by chance, we reject this null hypothesis. The testing of this initial hypothesis is done by using a randomisation procedure. We repeatedly (500 times) draw with replacement two samples of teeth of equal size. We then determine whether the frequencies of the observed differences for any given quantitative trait and any tooth category are as large as or larger than the actual difference calculated, assuming previous taxonomic

Table 2

Probabilities of observing, without previous taxonomic attributions and for each quantitative trait (MD and BL crown diameters, MD/BL index and crown area), resampled (500 times, with replacement) differences in means as large as, or larger than, the actual difference observed for each mandibular permanent tooth category.

Tableau 2. Probabilités d'observer, après ré-échantillonnage, ou *resampling*, (500 fois, avec remise) et sans attribution taxinomique préalable, des écarts entre les moyennes (diamètres coronaires MD et VL, indice MD/VL et aire occlusale) supérieurs ou égaux à ceux observés pour chaque type de dent mandibulaire permanente.

	M1	dm2	dm1	I2	I1
	Resampling (33)	Resampling (13)	Resampling (10)	Resampling (9)	Resampling (9)
Early <i>Homo</i> / <i>P. Robustus</i> ; MD	0%	0.2%	0%	5%	100%
Early <i>Homo</i> / <i>P. Robustus</i> ; BL	0%	0.6%	0.4%	63.2%	100%
Early <i>Homo</i> / <i>P. Robustus</i> ; Index	1.8%	100%	42.8%	7.2%	84.6%
Early <i>Homo</i> / <i>P. Robustus</i> ; Area	0%	0%	0.2%	5%	100%
	Resampling (23)	Resampling (12)	Resampling (8)	Resampling (6)	Resampling (9)
<i>P.boisei</i> / <i>P. robustus</i> ; MD	0%	0%	0%	0%	79.2%
<i>P. boisei</i> / <i>P. robustus</i> ; BL	5.6%	0%	5.6%	53.6%	49.4%
<i>P. boisei</i> / <i>P. robustus</i> ; Index	15.4%	32%	0%	0.6%	63.2%
<i>P. boisei</i> / <i>P. robustus</i> ; Area	0.5%	1.4%	0.4%	3.4%	40.6%

allocations. If this frequency is lower than 5% of the pairs of hypothetical samples, we conclude that the observed difference is unlikely to have occurred by chance and reject the null hypothesis (Table 2). The number of replications (500) is sufficient to detect significance at the $P = 0.05$ level for all but borderline cases [4].

The second step of our quantitative testing of the presence of early *Homo* at Kromdraai B is based on the comparison of KB 5223 values with those of early *Homo* and *P. robustus* reference samples, when the difference between them appeared significant (null hypothesis rejected during the preliminary step). This can be done by determining whether KB 5223 values fall outside the 95% confidence limits of the distributions representing the reference samples. The corresponding null hypothesis is that for each fossil reference sample and for each tooth, the value calculated for KB 5223 is included in the pattern of distribution in the fossil assemblage. Rejection of this null hypothesis supports the alternative hypothesis that KB 5223 represents another taxon. For any given quantitative trait, tooth category and reference sample, 500 random samples are selected with replacement. The 500 sample values were arrayed in a relative frequency distribution representing a reference sample. KB 5223 values are then plotted against the relative frequency distributions representing early *Homo* and *P. robustus* and used as a critical value. When a KB 5223 value falls outside a reference sample distribution, the null hypothesis of absence of difference is rejected. The KB 5223 value is used as critical to test the null hypothesis if it falls within the reference sample distribution. The proportion of lower or higher values in the reference sample distribution is then assessed in terms of one-tailed probability. If this exceeds 5%, the null hypothesis of the absence of difference cannot be rejected.

4. Results

4.1. Permanent first molars

The actual differences in means between the early *Homo* and *P. robustus* samples, for the four quantitative traits, is very unlikely to have occurred by chance (Table 2, Fig. 2). On the contrary, the observed differences between *P. robustus* and *P. boisei*, for the BL diameter and the MD/BL index, may well have oc-

curred by chance. The distributions representing early *Homo* and *P. robustus* reference samples do not overlap, except for the MD/BL index and the crown area where it is slight (Fig. 2). KB 5223 values fall outside the distribution representing *P. robustus*, except for the MD diameter (Fig. 2). For both the BL diameter and the MD/BL index, the null hypothesis of the absence of difference between KB 5223 and early *Homo* cannot be rejected. On the contrary, the null hypothesis of the absence of difference between KB 5223 and early *P. robustus* is clearly rejected. KB 5223 M₁ antimeres evince an important relative MD elongation, not seen in any *P. robustus* sample. At the same time, the crown area remains much smaller than any seen in a *P. robustus* sample.

KB 5223 M₁ antimeres show the presence of a postmetaconulid, or C7 sensu lato, combined with the absence of a C6 (Fig. 1), a condition which is known in specimens attributed to early *Homo* (e.g., OH 7 or Swartkrans SKX 257/258 M₁ antimeres), but not in Swartkrans specimens, which have been attributed to *P. robustus*. Furthermore, this combination of traits is not seen in M₁ teeth attributed to *P. boisei* [11] and *A. africanus*. By contrast, the presence of a C7 and/or postmetaconulid, and the absence of C6, is a morphological pattern seen in TM 1536, a right M₁ from Kromdraai. In the right DNH 35 erupting M₁ attributed to early *Homo* [9], a short fissure branching off the lingual fissure into the metaconid is seen (J.B.'s pers. obs.). This morphology, corresponding to minimal expression of the C7 defined by Wood and Abbott [11], is combined with a very small C6. In addition, KB 5223 M₁ antimeres possess a small and deep posterior fovea, bounded by a poorly developed distal marginal ridge. The morphology of this area contrasts with the well-defined posterior fovea often seen in *A. africanus*.

4.2. Deciduous molars

For both first and second deciduous molars, we conclude that the actual differences between the early *Homo* and *P. robustus* samples, except for the MD/BL indices (Table 2), is very unlikely to have occurred by chance. In these cases, the null hypothesis of absence of difference between KB 5223 dm₂ antimeres and *P. robustus* is clearly rejected. KB 5223 values fall within the early *Homo* distribution. On the contrary, with regard to the dm₁, the null hypothesis of absence

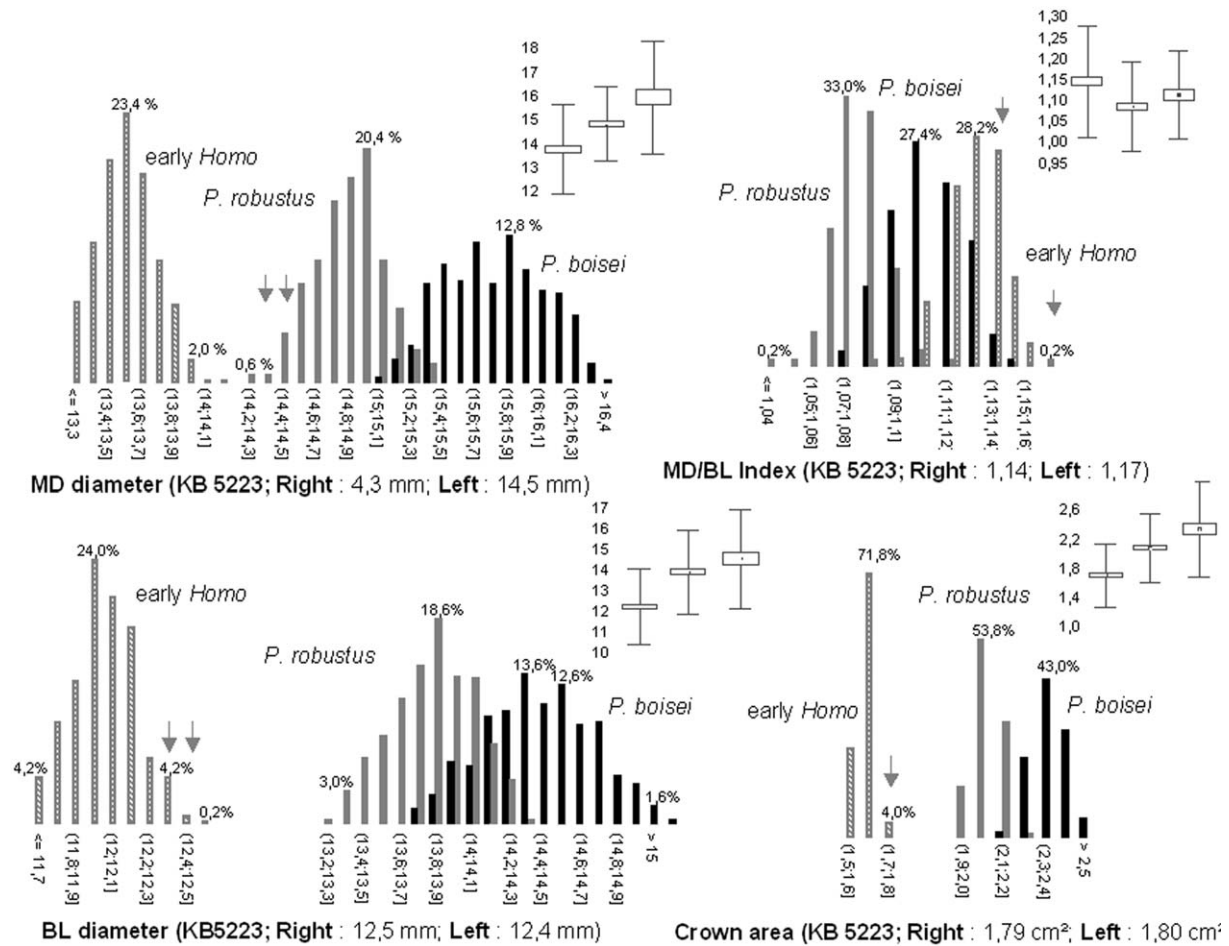


Fig. 2. Frequency histograms of means of MD and BL crown diameters (in mm), MD/BL index and occlusal area (MD × BL) (in cm²) calculated from 500 random samples of 16 teeth repeatedly drawn with replacement from each of the *Paranthropus robustus* ($n = 33$) and early *Homo* ($n = 32$) reference samples of permanent lower first molars. KB 5223 values are given. Mean values and two standard deviations are represented for, respectively from left to right, early *Homo*, *P. robustus* and *P. boisei*, for each trait, in the top right diagram.

Fig. 2. Histogrammes des fréquences des moyennes des diamètres MD et VL, de l'indice MD/VL et de l'aire occlusale (MD × VL) calculées pour 500 tirages aléatoires, avec remise de 16 dents pour chacun des deux échantillons de comparaison représentant la première molaire permanente de *Paranthropus robustus* ($n = 33$) et des premiers représentants du genre *Homo* ($n = 32$). Les valeurs obtenues pour KB 5223 sont indiquées. Les moyennes et les déviations standard sont représentées dans les figures situées en haut et à droite, pour chaque caractère, et pour, respectivement, de gauche à droite, early *Homo*, *P. robustus* et *P. boisei*.

of difference between KB 5223 and *P. robustus* cannot be rejected.

Most of the metaconid of KB 5223 dm₁ is not preserved whereas parts of the protoconid and hypoconid can be seen (Fig. 1). Nevertheless, KB 5223 dm₁ possesses only four principal cusps (the hypoconulid is absent), a condition suggesting similarities with early *Homo* from East Africa (e.g., ER 1507). The TM 1536 dm₁ antimeres, as well as all the scorable *Paranthropus* teeth, possess mostly five, if not six cusps. KB

5223 dm₁ also lacks the mesial accessory cuspule, a condition similar to early *Homo* (e.g., ER 1507), and to two other teeth from Kromdraai (TM 1536 and TM 1601). Conversely, the mesial accessory cuspule is present on all teeth attributed to *A. africanus* as well as on the Swartkrans *P. robustus* molars or the teeth attributed to *P. boisei* (e.g., ER 1477), the dm₁ having an asymmetrical mesial crown face. KB 5223 right dm₂ shows a slight postmetaconulid (a distal crest of the metaconid). Neither of KB 5223 dm₂ antimeres

possess a C6, nor is there a distal marginal ridge (Fig. 1). The presence of a postmetaconulid, combined with the absence of a C6, as seen in early *Homo* from Drimolen (DNH 35) (J.B.'s pers. obs.), contrasts with the morphological pattern seen in all *A. africanus* specimens, and in all specimens from Swartkrans attributed to *P. robustus*. Moreover, a C6 is present in specimens attributed to *P. boisei* (e.g., ER 1477 and ER 1820), but absent on the dm₂s from Koobi Fora attributed to early *Homo* (e.g., ER 1507 and ER 2601). Importantly, the TM 1536 dm₂ shows a C7 and also a small C6. In the KB 5223 dm₂ antimeres, we note the following: a 'doubled' anterior fovea (the anterior fovea of the TM 1536 right dm₂ is single and completely enclosed by a low trigonid crest). We also note deep mesiobuccal grooves ending abruptly in shallow pits (also on TM 1536). These observations contrast with what has been found in early *Homo* specimens from East Africa [14] though not from Drimolen (DNH 35, J.B.'s pers. obs.).

4.3. Permanent incisors

Importantly, the differences between early *Homo* and *P. robustus* samples, for both permanent incisors and all quantitative traits, are very likely to have occurred by chance (Table 2). In all cases, the null hypothesis of absence of difference cannot be rejected. Therefore, the second step of the resampling procedure is not justified. These results, incorporating new measurements, are in contradiction with previous observations, a long incisal edge being considered as a diagnostic feature of early *Homo* [7]. KB 5223 lower permanent incisors are mesiodistally smaller than all those from Swartkrans and Drimolen attributed to *P. robustus* (except SK 839/852 I₂) and those of early *Homo* represented at Koobi Fora and Swartkrans Members 1 or 1–2. Interestingly, the largest I₂ MD diameter is not found in *Homo* specimens, but in the only I₂ found at Drimolen so far, attributed to *P. robustus* (DNH 80). The obtuse corner of the distal half of the incisal edge with a 'mammellate' morphology was also described as a diagnostic feature of *Homo*, contrasting with the *P. robustus* 'sharp' morphology [7]. This *Homo*-like morphology can be seen in the KB 5223 right lateral lower permanent incisor found by Delson (Fig. 1). The distal half of the incisal edge of 'robust' specimens was described as having a "some-

what stronger inferior slope than the KB 5223 tooth", the slope being even "much sharper" in the Sterkfontein I₂ [18].

4.4. Deciduous and permanent canines

The lower left permanent and deciduous canines of KB 5223 are poorly preserved and incomplete. Due to incompleteness of the crowns, the principal dimensions of these two teeth cannot be measured and compared. The distal side of the crown of the deciduous canine (about 1/3) is missing. The permanent canine is represented by the upper half of its crown only. In this latter, the mesial and distal marginal ridges are visible on the lingual surface and the crown is asymmetrical.

5. Discussion

To test metrically the hypothesis of *Homo* at Kromdraai B, we have used a resampling procedure avoiding restrictive (and often false) assumptions about the underlying distributions of the qualitative traits. Doing so, we also avoided the problem inherent in investigations when a specimen is attributed to a hypodigm before fully exploring differences within and between supposedly different taxa. In our study, before examining KB 5223 values, we have tested hypotheses of difference between, on the one hand, early *Homo* and *P. robustus* samples, and, on the other hand, *P. robustus* and *P. boisei* samples. Quantitatively, when significant differences between early *Homo* and *P. robustus* have been found (not for permanent incisors), KB 5223 values clearly differing from *P. robustus* include: all M₁ values except the absolute MD diameter, all dm₂ values except the MD/BL index. Notably, the KB 5223 M₁ MD/BL index, one of the most diagnostic features that have been used in the past to identify early *Homo*, fall well outside the *P. robustus* distribution and within the one of early *Homo*. Together, this constitutes metric evidence for KB 5223 being attributed to early *Homo*.

The absence of C6, combined with the presence of C7, *sensu lato*, in the M₁ of the 2.4–2-Myr East African hominids, has been considered indicative of a 'non-robust' species [9, 18, 22]. This morphological pattern is found in most specimens attributed to early *Homo* from both southern and eastern Africa [7, 17, 18, 20–22] and has been used by Suwa et al. [18 (Table 4

and pp. 254–255]) to allocate mandibular molars from the Omo Valley to “robust or non robust categories”. Suwa et al. [18] included the absence of C6 combined with the presence of C in a total morphological pattern leading them to consider that “by circa 2.4 Myr, the postcanine dentition of the East African nonrobust lineage phenetically approximates the early *Homo* condition but lacks any specific affinities with *Australopithecus africanus*”. (op. cit., p. 275). Important morphological features distinguishing ‘robust’ species from early *Homo* are evident in KB 5223 deciduous molars: the absence of the hypoconulid and the mesial accessory cusplule on the four-cusped dm_1 , and the slight postmetaconulid combined with the lack of C6, and distal marginal ridge on the dm_2 . These features indicate close affinities between KB 5223 and some specimens from Koobi Fora attributed to early *Homo* (e.g., ER 1507). Because these important features are also lacking in *A. africanus*, they can be considered as derived, even when KB 5223 dm_2 displays a ‘doubled’ anterior fovea, a ‘primitive’ trait also seen in early *Homo* representatives (e.g., DNH 35).

TM 1536 is an incomplete mandible of a juvenile attributed to *P. robustus*. TM 1536 and KB 5223 are very close in M_1 occlusal morphology, with the absence of a C6 and the presence of a C7, sensu lato. However, TM 1536 does not display certain derived traits present in both early *Homo* and KB 5223, among which are the absence of the hypoconulid on the four-cusped dm_1 and the absence of the C6 on the dm_2 . With regard to the anterior dentition, an important diagnostic morphological feature of *Homo* permanent lower incisors is seen in KB 5223 right I_2 (Fig. 3): the obtuse corner of the distal half of the incisal edge, contrasting with the *P. robustus* ‘sharp’ morphology. All this constitutes morphological evidence for KB 5223 being attributed to the non-robust, ‘advanced’ genus *Homo*.

The absolute enamel thickness values of KB 5223 M_1 [8] fall within the 95% confidence limits obtained for early *Homo*[1]. Two absolute values of KB 5223 (LT and OT) [8] fall well outside the 95% confidence limits obtained for *P. boisei* [1]. Moreover, the KB 5223 LT lingual value is well below that observed for UR 501 right M_2 attributed to *Homo* ‘*rudolfensis*’ [2]. Four indices of average or relative enamel thickness have also been used. If we compute Z-scores to compare absolute or relative enamel thickness in KB 5223 (corrected values) [8] with either early *Homo* (values

in [1]) or extant humans (values in [8]), we find no significant differences to reject the null hypothesis of absence of differences. In other words, from the data published so far, we see no reason to consider absolute or relative enamel thickness in KB 5223 M_1 different from early *Homo* or extant humans.

The enamel accretionary pattern, as expressed by the length and orientation of the Brown of Striae of Retzius, is also of interest. KB 5223 M_1 displays Brown striae of Retzius that tend to become more highly angled relative to the enamel–dentine junction in the cervical region, than those of the molars of *P. boisei* and Swartkrans *P. robustus* specimens [8]. In terms of lower incisor spacing and distribution of perikymata, KB 5223 does not appear to be different from early *Homo* specimens [3].

6. Conclusions

The taxonomy of Kromdraai specimens has been the subject of much debate (see [10] for a review). Do the Kromdraai hominids represent a single taxon? Since most of the sample consists of isolated teeth, their taxonomic sorting should be systematically re-evaluated. After testing properly (by using resampling) the validity of some quantitative diagnostic features, here we suggest that KB 5223 does not group with *P. robustus*. Indeed, with regard to the MD diameter of the permanent incisors, a recent hominid find from Drimolen bridges the gap between reference samples, rendering this diagnostic feature unjustified. Moreover, after carefully considering the most diagnostic features that have been used in the past for the lower dentition, it appears that KB 5223 is morphologically and metrically indistinguishable from early *Homo* and, on the contrary, clearly distinct from *P. robustus*.

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References

- [1] A. Beynon, B. Wood, Variation in enamel thickness and structure in East African hominids, *Am. J. Phys. Anthropol.* 70 (1986) 177–193.
- [2] T. Bromage, F. Schrenk, F. Zonneveld, Paleoanthropology of the Malawi Rift: an early hominid mandible from the Chiwondo Beds, northern Malawi, *J. Hum. Evol.* 28 (1995) 71–108.
- [3] M.C. Dean, D. Reid, Perikymata spacing and distribution on hominid anterior teeth, *Am. J. Phys. Anthropol.* 116 (2001) 209–215.
- [4] B. Efron, R. Tibshirani, *An Introduction to the Bootstrap*, Chapman and Hall, New York, 1993.
- [5] F. Grine, Note on a new hominid specimen from Member 3, Kromdraai Formation, Transvaal, *Ann. Trans. Mus.* 33 (1982) 287–290.
- [6] F. Grine, *The Deciduous Dentition of the Kalahari San, the South African Negro and the South African Plio-Pleistocene Hominids*, Witwatersrand University, Johannesburg, 1984 PhD thesis.
- [7] F. Grine, New hominid fossils from the Swartkrans Formation (1979–1986 excavations): craniodental specimens, *Am. J. Phys. Anthropol.* 79 (1989) 409–449.
- [8] F. Grine, L. Martin, Enamel thickness and development in *Australopithecus* and *Paranthropus*, in: F. Grine (Ed.), *Evolutionary History of the 'Robust' Australopithecines*, Aldine de Gruyter, New York, 1988, pp. 3–42.
- [9] F.C. Howell, Hominidae, in: V. Maglio, H.B. Cooke (Eds.), *Evolution of African Mammals*, Harvard Univ. Press, Cambridge, Mass, USA, 1978, pp. 154–248.
- [10] K. Kaszycka, Status of Kromdraai. Cranial, Mandibular and Dental Morphology, Systematic Relationships, and Significance of the Kromdraai Hominids, *Cah. Paléanthropol.* CNRS, Paris, 2002.
- [11] A. Keyser, C. Menter, J. Moggi-Cecchi, T. Rayne Pickering, L. Berger, Drimolen: a new hominid-bearing site in Gauteng, South Africa, *S. Afr. J. Sci.* 96 (2000) 193–197.
- [12] L. Leakey, P. Tobias, J. Napier, A new species of the genus *Homo* from Olduvai Gorge, *Nature* 202 (1964) 7–9.
- [13] J. Moggi-Cecchi, P. Tobias, A. Beynon, The mixed dentition and associated skull fragments of a juvenile fossil hominid from Sterkfontein, South Africa, *Am. J. Phys. Anthropol.* 106 (1998) 425–465.
- [14] F. Ramirez Rozzi, Can enamel microstructure be used to establish the presence of different species of Plio-Pleistocene hominids from Omo, Ethiopia? *J. Hum. Evol.* 35 (1998) 543–576.
- [15] J. Robinson, *The Dentition of the Australopithecinae*, 9, Transvaal Museum Memoir, Pretoria, 1956.
- [16] F. Schrenk, T. Bromage, C. Betzler, U. Ring, Y. Juwayeyi, Oldest *Homo* and Pliocene biogeography of the Malawi rift, *Nature* 365 (1993) 833–936.
- [17] G. Suwa, *A comparative analysis of hominid dental remains from the Shungura and Usno Formations, Omo Valley, Ethiopia*, University Microfilms, Ann Arbor, Michigan, USA, 1990.
- [18] G. Suwa, T. White, F.C. Howell, Mandibular postcanine dentition from the Shungura formation, Ethiopia: crown morphology, taxonomic allocations, and Plio-Pleistocene hominid evolution, *Am. J. Phys. Anthropol.* 101 (1996) 247–282.
- [19] J.F. Thackeray, D. de Ruiter, L. Berger, N. van der Merwe, Hominid fossils from Kromdraai: a revised list of specimens discovered since 1938, *Ann. Transv. Mus.* 38 (2001) 43–56.
- [20] P. Tobias, *Olduvai Gorge, vols. 4A and AB. The Skulls, Endocasts and Teeth of Homo habilis*, Cambridge University Press, Cambridge, UK, 1991.
- [21] B. Wood, *Koobi Fora Research Project, Vol. 4, Hominid Cranial Remains*, Oxford University Press, Oxford, 1991.
- [22] B. Wood, S. Abbott, Analysis of the dental morphology of Plio-Pleistocene hominids. I. Mandibular molars: crown area measurements and morphological traits, *J. Anat.* 136 (1983) 197–219.