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DENTAL EVIDENCE FOR PHYLOGENETIC RELATIONSHIPS OF MIDDLE PALEOLITHIC HOMINIDS

by

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Teeth play an important role in general evolutionary studies, for a number of reasons. Firstly the teeth are usually better preserved, and so are present in larger numbers than any other part of the skeleton. Secondly, teeth complete their development early in life when the organism is well protected from external stresses. The dental phenotype, shown in tooth size and morphology, then provides a reliable blueprint of the underlying genotype, while modification through function and disease can be easily recognised. Permanent teeth from juvenile and adult specimens of both sexes can then be pooled for study, whereas in studies of the bony skeleton, age is an important variable. This since skeletal characteristics are continually modified, initially by growth during childhood and adolescence, and by remodelling in response to function and disease in adult life. For these reasons, dental characteristics of the Neandertals have played a significant role in studies of their phylogenetic relationships. Early researchers such as GORJANOVIC-KRAMBERGER (1906, 1907), KEITH (1925), KEITH and FOWLES (1911), McCOWN and KEITH (1939) and WEIDENREICH (1937) gave considerable weight to morphological traits of the dentition, in classifying early hominids. KEITH (1925) following GORJANOVIC-KRAMBERGER (1907) emphasised the specialized nature of the Neandertal dentition especially in such features as taurodontism, large size of lingual tubercles and Carabelli's trait. They considered that such features excluded Neandertals from the ancestry of modern *Homo sapiens sapiens*. WEIDENREICH (1937), on the other hand, described the Neandertals, as represented by Krapina, Ehringsdorf and Le Moustier, as intermediate between Sinanthropus and modern populations in tooth size and morphology. He stressed the greater proximity of the Neandertals to modern populations in canine and premolar morphology and root size. He noted that the Neandertals showed an accentuation of such features present in Sinanthropus as lingual tubercles and taurodontism, but considered this a possible expression of regional variation as well as evolutionary stade. Subsequently, less attention has been paid to morphological traits in the dentition as classificatory tools, and tooth size has been incresingly used to this end (BRACE, 1979; WOLPOFF, 1980; SMITH, 1977a, 1977b; FRAYER, 1978, 1984).

However, the use of tooth size for establishing phylogenetic relationships is problematic for a number of reasons. There is general recognition that in using dental measurements to compare phenotypes, only unworn teeth can be used to establish mesiodistal diameters of the crowns of the teeth, and that even buccolingual diameters are

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affected by severe attrition. However examination of the samples used by various authors (BRACE, 1979; FRAYER, 1978; SMITH, 1977a; WOLPOFF, 1980), shows that interpretations of what constitutes an unworn tooth are very liberal. Moreover in most studies of fossil teeth, data for males and females are pooled, since the majority of fossil specimens suitable for measurement are either juvenile or fragmentary and difficult to sex reliably.

It must be recognised however that this introduces an additional source of error, since tooth size is dimorphic, especially for buccolingual dimensions (GARN *et al.*, 1967; SMITH, 1977). Studies on living populations further indicate that tooth size alone should not be used as a measure of genetic distance. Amerindian populations show variation of as much as 30 % in tooth size, and include some of the largest and smallest toothed populations alive (SMITH, 1982), despite their large number of common genetic traits.

Dental traits give results that are more compatable with conventional measures of population distance, as calculated from blood groups and serum proteins (DAHLBERG, 1963; SCOTT *et al.*, 1983; SMITH; 1977c; SOFAER *et al.*, 1986; GREENBERG *et al.*, 1986). They also have an additional advantage in that they are not dimorphic (SOFAER *et al.*, 1986; SMITH, 1977c), and are also present in the deciduous dentition.

Relatively few studies have been published on evolutionary trends in the deciduous dentition (BRABANT, 1965; JORGENSEN, 1956; KOENIGSWALD, 1967; ROBINSON, 1956; SMITH, 1978). Studies based on living populations have shown that they may have considerable value, both in increasing the data base on dental traits, and so group affinities, and in providing information on their phylogeny. In so far as dental traits are concerned, the deciduous incisors, canines and second molars resemble the succeeding teeth, and so provide additional information on the dental phenotype of a specific group. Since they develop *in utero* and in early infancy, they are largely protected from environmental insults in development. In addition because they do develop at such an early age, the deciduous teeth are generally considered to be more conservative in morphology than the permanent teeth.

The differences that are present in trait expression between the deciduous and permanent teeth of any one population appear to express the phylogenetic history of that trait (KEISER, 1984; SAUNDERS and MAYHALL, 1982; SMITH *et al.*, 1987; TOWNSEND *et al.*, 1986). Those traits that are more common on the deciduous teeth than on their permanent successors, appear to be more "archaic" and appear earlier in ontogenesis than traits that are more frequent on the permanent teeth. Comparison of dental traits in the deciduous and permanent teeth of the Neandertals may then provide an additional means of tracing phylogenetic relationships between them and antecedent and succeeding populations.

For many reasons the Near Eastern Mousterian hominid sample provides a good starting point for dental studies of *sapiens*-neandertal affinities. While there are still some difficulties with the exact chronology of the sites (BAR-YOSEF and VANDERMEERSCH, 1981; JELINEK, 1981 [1]), all were found associated with the same Middle Paleolithic culture (Mousterian), and utilised a similar habitat. The majority of the specimens also come from a very limited geographic region with five of the six sites studied falling within a 30 km radius. In terms of skeletal morphology they fall into two clearly defined groups. There is general consensus that the hominids at Tabun-Amud-Kebara-Shanidar are *Homo sapiens neandertalensis* while the Qafzeh-Skhul group belong to *Homo sapiens sapiens* (McCOWN and KEITH, 1939; SMITH and ARENSBURG, 1977; STRINGER *et al.*, 1982; SUZUKI and TAKAI, 1970; TRINKAUS, 1983; VANDERMEERSCH, 1981). They therefore provide a strictly defined sample for examining population replacement versus evolution *in situ*.

[1] But see new dates for Qafzeh and Kebara in VALLADAS *et al.*, 1987, 1988.

In their detailed comparison of the hominids from Tabun and Skhul, McCOWN and KEITH (1939) defined a number of features that they considered characteristic of Neandertal dentitions. Their classification was based largely on the teeth from Ehringsdorf, St. Brelade (Jersey) and Krapina, and morphological traits characterized as "Neandertal" included taurodontism, large lingual tubercles (premolarization) on anterior teeth, wrinkled enamel on molars and some expression of Carabelli's complex on most molars. They characterized teeth as large, especially the incisors, and thick buccolingually. All of these features were present to some degree in the Tabun teeth, except for wrinkled enamel, while the Skhul teeth lacked large lingual tubercles and showed only a minor degree of taurodontism. The Tabun and Skhul specimens also differed in lower molar root length. This was longer in the second molar than in the first in Tabun 2, while the reverse size relationship applied to the Skhul molars.

Examination of dental traits and molar root size in the more recently discovered *Homo sapiens sapiens* specimens from Qafzeh shows them to resemble those of Skhul, while the Neandertal teeth from Shanidar and Kebara resemble those of Tabun. The adult Neandertal from Amud (Amud I) has exceptionally small teeth except for the buccolingual diameters of the anterior teeth. It also has a peg shaped third molar. There is little difference in length of the roots of the lower first and second molars, and only minor degree of taurodontism. However, incisor and first molar morphology resembles that of the other Neandertals, and the dentition of the infant from Amud clearly falls into the Neandertal category (SMITH and ARENSBURG, 1977).

When the Near Eastern hominids are compared with European Neandertals, of the last glaciation, there is a clear separation between the two Neandertal groups and the early *Homo sapiens sapiens* group in both tooth size and trait expression. Both European and Near Eastern Neandertal permanent upper incisors and canines normally have large lingual tubercles, and these are well developed even in the relatively small teeth from Hortus. Taurodontism is more frequently present, and more pronounced than in *Homo sapiens sapiens* (VERDENE *et al.*, in prep.); the second molars are usually larger than the first molars, with the differences marked in root length as well as crown size; all four cusps are normally present in the upper second molars; although third molars may show reduction of the hypocone. Carabelli's cusp or pit is frequently present on second and third molars as well as first molars. In the early *sapiens* group the lingual tubercles are smaller or absent on the incisors, Carabelli's complex is usually limited to the first molar; taurodontism is less pronounced and first molar root length is usually as long as or longer than that of the second molar.

The deciduous incisors and canines of all three groups (Near East Neandertals, and *Homo sapiens sapiens* as well as European Neandertals) lack the large lingual tubercles of the permanent teeth. Tubercles, when present, tend to be relatively small. They are sometimes present on the canines, as in the infants from Pech de L'Aze and Chateauneuf, more rare on the lateral incisors and extremely rare on the central incisors. The lingual surface usually shows a large but smooth convexity on the basal half. In contrast, Carabelli's cusp is present in similar frequencies in the upper second deciduous molar and first permanent molar. In the lower second deciduous molars and first permanent molars, 6th cusps and 7th cusps are also present in similar frequencies.

The main differences between the deciduous teeth of the *Homo sapiens sapiens* group and the two Neandertal groups lies in incisor and canine outline, and first molar morphology. The Neandertal incisors and canines show greater reduction of marginal lobes, and greater frequency of mesial and distal styles, so that the incisal edge is more pointed. The roots are broader mesiodistally but flattened buccolingually. The upper first deciduous molar in Neandertals also tends to show narrowing of the distance between the buccal and lingual cusps on the distal portion of the tooth, while the crown sits obliquely to the main axis of the tooth.

Tooth size also discriminates between the three groups (Tables 1-6). In the permanent teeth, mean values for incisor tooth size in the Near Eastern *Homo sapiens sapiens* are slightly smaller buccolingually than in the Neandertals, while first molar size is significantly larger ($p < 0.05$), when the groups are compared using one way analysis of variance. Size differences in the upper buccolingual diameter of the lateral incisor are statistically significant between the Near Eastern *Homo sapiens sapiens* and European Neandertals but not between the Near Eastern *Homo sapiens sapiens* and Near Eastern Neandertals (Tables 1-4).

Within the Neandertals themselves there is considerable variation of incisal buccolingual width. Both upper and lower incisors in the European Neandertal group from Hortus are smaller buccolingually and mesiodistally than those of Near Eastern *Homo sapiens sapiens*.

The deciduous teeth show no significant size differences in the incisors or canines and especially small teeth are found both in Near Eastern (Shanidar 7), and European (Subulyuk) Neandertals. Deciduous molar size relationships are however, similar to those found in the permanent teeth. The early *Homo sapiens sapiens* deciduous molars are larger than those of the Near Eastern and European Neandertals, and the differences are statistically significant for the dm1 and dm2 ($P < 0.05$).

A number of researchers have proposed a temporal gradient in Neandertal tooth size (De LUMLEY, 1972, 1976; F. SMITH, 1977; SMITH, 1977a, 1977b). Tooth size in most ante-Neandertals and early Neandertals from the Riss-Würm is larger than that of Neandertals, from Würm 1 and 2. De LUMLEY (1972), and F. SMITH (1984), consider that a further reduction in Neandertal tooth size took place towards the end of Würm 2 based on findings from Hortus and Vindija respectively. However, TRINKAUS (1983) found no reduction of tooth size over the 20,000 year period represented at Shanidar, and tooth size in individual specimens varies widely.

Spy, Hortus, Vindija and Amud have exceptionally small molars relative to other Neandertals, with cusp reduction in the second and third molars. Hortus incisors are small, but all incisors and canines have distinct lingual tubercles. At Shanidar, buccolingual diameters appear to be exceptionally large, both in relation to molar size, and in relation to deciduous tooth values from the same site. At Skhul and Qafzeh, both permanent and deciduous tooth size varies widely with specimens from both sites covering the entire range of values recorded for Neandertal teeth, with the exception of buccolingual diameter of incisors.

The size of the deciduous molar teeth, but not the incisors in these three groups, shows a similar pattern to that found for the permanent teeth. For the incisors no significant differences in tooth size were found, and indeed the Shanidar deciduous incisors are especially small. This contrasts to the situation found at all other sites where both deciduous and permanent teeth were recovered, where there is a good correspondance between deciduous and permanent tooth size and proportions. While as much as 20,000 years may separate the various Neandertal finds excavated from this cave, TRINKAUS (1983) has grouped the infant (Shanidar 7), with the geologically older finds so that temporal differences cannot account for the discrepancy between deciduous and permanent tooth size at this site.

The major distinctive metric features of Neandertal teeth are the large buccolingual diameters of the incisors, and the ratio of second molar to first molar root length. These are plesiomorphic traits and the Neandertal teeth show no distinctive characteristics in size that put them outside the general evolutionary sequence of *Homo*. However, the marked accentuation of certain features such as lingual tubercles and taurodontism appear to be specific to the Neandertal permanent dentition. They are far less developed in the Neandertal deciduous dentition, and in earlier fossil hominids. By analogy to other traits this would

suggest that they are newly acquired traits (autapormorphous) rather than "archaic" ones (plesiomorphous). In addition, the Neandertal deciduous dentition is characterized by a distinctive upper first molar cusp form, that does not appear to be present in earlier *Homo erectus* (TILLIER, 1980), or in *Homo sapiens sapiens* (SMITH and ARENSBURG, 1977).

The morphology as well as size of the early Near Eastern *Homo sapiens sapiens* teeth is then strikingly different from that of the Neandertals from the Near East or Europe. The dental findings, like the skeletal findings reported by SPRINGER *et al.* (1984), point to a greater resemblance between European and Near Eastern Neandertals than between Near Eastern *Homo sapiens sapiens* and Near Eastern Neandertals, and do not support the hypothesis of transition between Neandertals and *Homo sapiens sapiens* in the Near East.

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REFERENCES

BAR-YOSEF O. and VANDERMEERSCH B., 1981. Notes concerning the possible age of the Mousterian layers in Qafzeh Cave. *In: Colloques Internationaux du CNRS*, n° 598, Paris.

BRABANT H., 1965. Observations sur l'évolution de la denture humaine en Europe Occidentale. *Bulletin de Groupement International de Recherche Scientifique Stomatologique* 8: 235-302.

BRACE C.L., 1979. Krapina "Classic" Neanderthals, and the evolution of the European face. *Journal of Human Evolution* 8: 527-550.

BUTLER P.M., 1967. Comparison of the development of the second deciduous molar and first permanent molar in man. *Archives of Oral Biology* 12: 1245-1260.

DAHLBERG A.A., 1963. Analysis of the American Indian dentition: *In:* D.R. BROTHWELL (ed.), *Dental Anthropology*, Pergamon Press, Oxford, pp. 149-177.

FRAYER D., 1978. *Evolution of the dentition in Upper Paleolithic and Mesolithic Europe*. Publications in Anthropology, University of Kansas.

FRAYER D., 1984. Late Pleistocene and Early Holocene Europe. *In:* F.H. SMITH and F. SPENCER (eds.), *The Origins of Modern Humans*, Alan R. Liss, Inc. New York, pp. 211-250.

GARN S.M., LEWIS A.B., SWINDLER D.R. and KEREWSKY R.S., 1967. Genetic control of sexual dimorphism in tooth size. *Journal of Dental Research* 46: 963-972.

GORJANOVIC-KRAMBERGER K., 1906. *Der diluviale Mensch von Krapina in Kroatien: Ein Beitrag zur Palaoantropologie*. Kriedel, Wiesbaden.

GORJANOVIC-KRAMBERGER, 1907. Die Kronen und Wurzeln der Mahlzahne des *Homo primigenius* und ihre genetische Bedeutung. *Anatomischer Anzeiger* 31: 97-134.

GREENBERG J.H., TURNER C.G. and VEGURA S.L., 1986. The settlements of the Americas: a comparison of the linguistic, dental and genetic evidence. *Current Anthropology* 27: 477-497.

JELINEK A.J., 1981. The middle Paleolithic in the southern Levant from the perspective of the Tabun cave. *In: Colloques Internationaux du CNRS*, n° 598, Paris.

JORGENSEN K.D., 1956. The deciduous dentition. *Acta Odontologica Scandinavia*, 14, Supp., 20.

KEISER J.A., 1984. An analysis of the Carabelli trait in the mixed deciduous and permanent human dentition. *Archives of Oral Biology* 29: 403-406.

KEISER J.A., GROENEWELD H.T. and PRESTON C.B., 1986. Fluctuating dental asymmetry as a measure of odontogenic canalization in man. *American Journal of Physical Anthropology* 71: 437-444.

KEITH A., 1925. *The Antiquity of Man.* Willian and Norgate, Ltd., London.

KORENHOF C.A.W., 1982. Evolutionary trends of the inner enamel anatomy of deciduous molars from Sangiran (Java, Indonesia). *In:* B. KURTEN (ed.), *Teeth, Form, Function and Evolution*, Columbia University Press, New York, pp. 350-355.

KRAUS B.S., 1963. Morphogenesis of deciduous molar pattern in man. *In:* D.R. BROTHWELL (ed.), *Dental Anthropology*, Pergamon Press, Oxford, pp. 87-104.

LUMLEY M.A. de, 1972. *Les Néandertaliens de la grotte de l'Hortus.* Etudes Quaternaires, Mémoire n° 1, pp. 375-385.

LUMLEY M.A. de, 1976. Les Néandertaliens dans le Nord et le Centre. *La préhistoire française*, Tome 1, CNRS, Paris, pp. 588-594. Quaternaires.

McCOWN T. and KEITH A., 1939. *The Stone Age of Mount Carmel.* Vol. II, Clarendon Press, Oxford.

PATTE E., 1959. La dentition des Néanderthaliens. *Annales de Paléontologie* 45: 223-301.

ROBINSON J., 1956. *The Australopithecine dentition.* Memoirs of the Transvaal Museum, Pretoria.

SAUNDERS S.R. and MAYHALL J.T., 1982. Fluctuating asymmetry of dental morphological traits: new interpretations. *Human Biology* 54: 789-799.

SCOTT G.R., POTTER R.H.Y., NOSS J.F., DAHLBERG A.A. and DAHLBERG T., 1983. The dental morphology of Pima Indians. *American Journal of Physical Anthropology* 61: 13-31.

SENYUREK M., 1959. *A study of the deciduous teeth of the fossil Shanidar infant – A comparative study of the milk teeth of fossil men.* Publications of the Faculty of Languages, History and Geography, University of Ankara, 128: 5-174.

SMITH F.H., 1984. Fossil hominids from the upper Pleistocene of Central Europe and the origin of modern Europeans. *In:* F.H. SMITH and F. SPENSER (eds.), *The Origins of Modern Humans: A World Survey of the Fossil Evidence*, Alan R. Liss, Inc., New York, pp. 137-209.

SMITH P. and ARENSBURG B., 1977. The Mousterian infant from Kebara. *In:* O. BAR-YOSEF and B. ARENSBURG (eds.), New Discoveries in the Carmel Range, *Israel Exploration Journal* 13, Jerusalem, pp. 164-176.

SMITH P., 1977a. Regional variation in tooth size and pathology in fossil hominids. *American Journal of Physical Anthropology* 47: 459-466.

SMITH P., 1977b. Selective pressures and dental evolution in hominids. *American Journal of Physical Anthropology* 47: 453-458.

SMITH P., 1977c. Variation in dental traits within population. *In:* A. DAHLBERG and T. GRABER (eds.), Oro-Facial Growth and Development, *World Anthropology*, Mouton Press, pp. 171-181.

SMITH P., 1978. Evolutionary changes in the deciduous dentition of Near Eastern Populations. *Journal of Human Evolution* 7: 401-408.

SMITH P., 1982. Dental reduction: selection or drift. *In:* B. KURTEN (ed.), *Teeth, Form, Function and Evolution*, Columbia University Press, pp. 366-379.

SMITH P., KOYOUMIDJISKY-KAYE E., KALDERON W. and STERN D., 1987. Directionality of dental trait frequency between human second deciduous and first permanent molars. *Archives of Oral Biology* 32: 5-9.

SOFAER J., SMITH P. and KOYOUMIDJISKY-KAYE E., 1986. Affinities between contemporary and skeletal Jewish and non-Jewish groups based on tooth morphology. *American Journal of Physical Anthropology* 70: 265-275.

STRINGER C.B., HUBLIN J.J. and VANDERMEERSCH B., 1984. The Origin of anatomically modern humans in western Europe. *In:* F.H. SMITH and F. SPENSER (eds.), *The Origins of Modern Humans: A World Survey of the Fossil Evidence*, Alan R. Liss, Inc. New York, pp. 51-135.

SUZUKI H. and R. TAKAI (eds.), 1970. *The Amud Man and His Cave Site*. University of Tokyo Press.

THOMA A., 1963. The dentition of the Subalyuk Neandertal child. *Zeitschrift für Morphologie und Anthropologie* 54: 127-150.

THOMA A. and VALLOIS H.V., 1977. Les dents de l'homme de Rabat. *Bulletin et Mémoires de la Société d'Anthropologie de Paris* t-4 ser. XIII: 31-58.

TILLIER A.M., 1980. Les dents d'enfant de Ternifine (Pleistocène moyen d'Algérie). *L'Anthropologie* 84/3: 413-421.

TOWNSEND G., HIROYUKI Y. and SMITH P., 1986. The metaconule in Australian aboriginals: an accessory tubercle on maxillary molar teeth. *Human Biology* 58: 851-862.

TRINKAUS E., 1983. *The Shanidar Neandertals*. Academic Press, New York, 502 pages.

VALLADAS H., JORON J.L., VALLADAS G., ARENSBURG B., BAR-YOSEF O., BELFER-COHEN A., GOLDBERG P., LAVILLE H., MEIGNEN L., RAK Y., TCHERNOV T., TILLIER A.M., VANDERMEERSCH B., 1987. Thermoluminescence dates for the Neanderthal burial site at Kebara, Israel. *Nature* 330: 159-160.

VALLADAS H., REYSS J.L., JORON J.L., VALLADAS G., BAR-YOSEF O. and VANDERMEERSCH B., 1988. Thermoluminescence dating of Mousterian "Proto-Cro-Magnon" remains from Israel and the origin of modern man. *Nature* 331: 614-616.

VANDERMEERSCH B., 1981. Les hommes fossiles de Qafzeh (Israel). *Cahiers de Paléontologie* CNRS, Paris.

WEIDENREICH F., 1937. The dentition of *Sinanthropus pekinensis*: a comparative odontography of the hominids. *Paleontologia Sinica*.

WOLPOFF M.H., 1980. *Paleoanthropology*. Knopf, New York.

TABLE 1

Upper Mesiodistal diameter

	M3	M2	M1	PM2	PM1	C	I2	I1	Sample
Mean	941	1040	1128	703	764	838	783	1001	
Min	880	880	990	655	692	750	670	850	Israel *H. s. sapiens*
Max	1005	1220	1240	750	870	952	880	1130	
S.D.	5.0	11.5	6.3	3.3	6.5	5.1	7.7	8.0	
No cases	5	9	18	9	9	11	11	13	
Mean	950	1215	1100	694	751	820	708	902	
Min	665	1180	1050	655	700	780	670	820	Israel and Iraq,
Max	1280	1280	1200	740	870	870	770	1000	*H.s. neandertalensis*
S.D.	18.8	3.0	5.0	3.5	6.6	3.8	4.0	7.0	
No cases	7	8	7	6	7	6	5	5	
Mean	968	1032	1081	731	752	839	799	935	
Min	790	945	1000	650	630	740	585	800	Europe
Max	1230	1150	1200	800	881	929	900	1000	*H.s. neandertalensis*
S.D.	12.6	6.3	5.1	5.0	6.0	5.5	8.3	6.6	
No cases	12	14	14	12	16	16	12	11	
Mean	978	1038	1105	736	754	820	737	920	
Min	835	914	980	615	675	710	640	860	Europe *H.s. sapiens*
Max	1105	1180	1215	1094	940	929	882	1000	
S.D.	10.2	7.7	7.0	11.8	69.8	6.8	8.3	3.0	
No cases	7	14	15	13	15	11	8	11	

TABLE 2

Upper Buccolingual diameter

	M3	M2	M1	PM2	PM1	C	I2	I1	Sample
Mean	1187	1202	1225	1019	1035	931	745	804	Israel *H.s. sapiens*
Min	1120	1052	1120	900	973	800	620	683	
Max	1250	1275	1330	1100	1095	1035	850	870	
S.D.	4.9	6.8	6.1	6.7	3.8	7.7	7.1	6.4	
No cases	5	9	18	9	9	11	10	11	
Mean	1149	1100	1224	982	1022	922	778	810	Israel
Min	935	1050	1120	900	930	840	710	750	*H.s. neandertalensis*
Max	1260	1200	1290	1080	1080	985	840	830	
S.D.	14.5	5.0	5.0	6.8	4.9	6.1	5.9	3.4	
No cases	7	8	7	6	7	6	5	5	
Mean	1168	1243	1194	1030	1013	953	811	812	Europe
Min	950	1030	985	915	840	840	710	740	*H.s. neandertalensis*
Max	1380	1357	1300	1100	1120	1060	890	893	
S.D.	13.3	9.7	7.9	5.4	7.9	6.3	5.4	4.6	
No cases	12	14	15	13	17	16	12	10	
Mean	1198	1248	1222	987	983	918	699	761	Europe *H.s. sapiens*
Min	1060	1110	1105	890	870	775	640	715	
Max	1315	1370	1354	1135	1092	1063	760	860	
S.D.	9.6	9.2	6.8	6.6	7.2	10.0	4.2	3.9	
No cases	8	14	15	14	15	12	10	13	

TABLE 3

Lower Mesiodistal diameter

	M3	M2	M1	PM2	PM1	C	I2	I1	Sample
Mean	1156	1089	1200	771	764	792	657	565	
Min	1050	975	1050	720	580	665	589	450	Israel *H.s. sapiens*
Max	1120	1210	1350	830	850	910	740	675	
S.D.	7.8	9.1	8.6	3.6	9.6	7.5	5.7	8.3	
No cases	6	7	14	7	7	8	8	9	
Mean	1135	1126	1140	723	747	803	772	535	
Min	1030	975	1050	670	710	770	700	480	Israel and Iraq
Max	1220	1300	1350	776	835	1110	837	650	*H.s. neandertalensis*
S.D.	6.7	8.6	5.4	3.6	4.4	1.3	6.0	5.9	
No cases	10	10	9	7	6	7	6	6	
Mean	1165	1157	1133	742	762	748	625	520	
Min	990	1045	983	500	550	540	460	360	Europe
Max	1300	1251	1240	850	862	860	750	690	*H.s. neandertalensis*
S.D.	7.0	5.4	5.8	8.7	7.8	8.6	8.5	10.7	
No cases	18	18	21	17	17	17	11	7	
Mean	1121	1142	1186	727	733	776	629	560	
Min	1000	950	1030	650	620	680	500	660	Europe *H.s. sapiens*
Max	1280	1280	1290	831	869	834	777	650	
S.D.	11.4	9.7	6.8	5.6	6.6	5.1	8.2	7.0	
No cases	7	18	21	11	13	10	13	10	

TABLE 4

Lower Buccolingual diameter

	M3	M2	M1	PM2	PM1	C	I2	I1	Sample
Mean	1061	1090	1159	880	891	839	717	669	
Min	900	987	1050	790	770	700	595	503	Israel *H.s. sapiens*
Max	1195	1195	1245	965	1100	970	800	770	
S.D.	10.3	8.1	6.3	6.4	10.6	7.6	6.9	7.5	
No cases	6	7	12	7	8	8	8	9	
Mean	1078	1109	1131	910	915	872	772	704	
Min	900	1030	1020	830	850	750	700	635	Israel and Iraq
Max	1260	1270	1230	1060	945	1033	837	770	*H.s. neandertalensis*
S.D.	8.7	6.8	7.2	7.6	3.3	8.3	6.0	5.1	
No cases	10	10	8	7	7	6	6	6	
Mean	1120	1082	1070	898	874	859	756	706	
Min	845	970	934	663	614	730	687	680	Europe
Max	1330	1230	1180	1050	980	990	820	722	*H.s. neandertalensis*
S.D.	11.8	8.0	6.6	10.5	8.9	7.8	4.1	1.7	
No cases	18	17	26	17	16	16	9	5	
Mean	1096	1110	1108	861	848	892	689	638	
Min	995	1000	1000	800	780	800	600	590	Europe
Max	1245	1201	1180	945	971	980	787	738	*H.s. sapiens*
S.D.	10.6	8.3	5.2	5.3	5.3	6.7	4.6	4.1	
No cases	7	18	21	11	13	10	14	12	

TABLE 5a

Upper Mesiodistal diameter

dm2					dm1					dc					dI2					dI1					
N	X	SD	Min	Max	N	X	SD	Min	Max	N	X	SD	Min	Max	N	X	SD	Min	Max	N	X	SD	Min	Max	
6	962	2.2	920	980	7	830	6.2	750	940	6	757	5.8	750	860	5	652	3.3	620	705	5	770	3.4	710	793	Israel *H.s.sapiens*
4	922	2.7	890	950	5	763	2.0	742	790	3	755	3.7	720	795	2	586	2.3	570	602	5	764	3.3	725	810	Israel *H.s. neandertalensis*
8	939	6.1	880	1075	8	792	5.4	690	845	6	743	4.2	700	815	5	606	2.8	560	635	6	738	4.0	675	785	European *H.s. neandertalensis*

TABLE 5b

Lower Mesiodistal diameter

dm2					dm1					dc					dI2					DI1					
N	X	SD	Min	Max	N	X	SD	Min	Max	N	X	SD	Min	Max	N	X	SD	Min	Max	N	X	SD	Min	Max	
8	1107	4.8	1015	1157	7	904	2.3	877	944	5	655	5.4	590	740	4	499	3.7	460	550	1	440				Israel *H.s. sapiens*
5	1047	6.1	1000	1130	4	877	2.1	850	895	4	666	4.8	600	715	4	538	2.9	507	570	3	484	2.1	460	502	Israel and Iraq *H.s. neandertalensis*
11	1056	.4	1000	1130	9	856	5.2	760	910	5	638	6.1	570	720	2	535	7.7	480	590	4	475	5.0	400	510	European *H.s. neandertalensis*

TABLE 6a

Upper Buccolingual diameter

dm2					dm1					dc					dI2					dI1					
N	X	SD	Min	Max	N	X	SD	Min	Max	N	X	SD	Min	Max	N	X	SD	Min	Max	N	X	SD	Min	Max	
6	1068	3.7	1000	1113	7	900	4.7	837	978	5	692	5.2	655	780	5	599	4.7	510	612	4	556	1.7	540	580	Israel *H.s. sapiens*
4	1021	2.9	980	1050	5	930	3.3	880	970	3	720	3.0	690	750	2	540	1.4	530	550	5	604	1.1	590	620	Israel and Iraq *H.s. neandertalensis*
8	1055	3.5	1014	1115	8	920	3.9	879	985	6	601	3.6	570	660	2	410	7.0	420	520	4	436	4.6	370	480	European *H.s. neandertalensis*

TABLE 6b

Lower Buccolingual diameter

dm2					dm1					dc					dI2					dI1					
N	X	SD	Min	Max	N	X	SD	Min	Max	N	X	SD	Min	Max	N	X	SD	Min	Max	N	X	SD	Min	Max	
8	981	5.8	910	1067	7	748	5.1	690	835	4	613	7.8	550	724	4	400	1.2	480	502	1	445				Israel *H.s. sapiens*
5	930	4.0	900	1000	4	751	1.6	730	770	3	600	3.6	560	630	4	499	1.5	485	520	3	470	1.0	460	480	Israel and Iraq *H.s. neandertalensis*
10	935	4.2	898	1040	9	745	2.0	710	770	6	601	3.6	570	660	2	410	7.0	420	520	4	436	4.6	370	480	European *H.s. neandertalensis*