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A Comparison of the Krapina Lower Facial Remains to an Ontogenetic Series of Neandertal Fossils

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Abstract

The Krapina facial remains are associated with the Neandertals based on a number of descriptive morphological traits, but the degree to which these fossils correspond to the morphology of other Neandertals has largely been assumed rather than explicitly examined. One reason initially was the dearth of an ontogenetic series of Neandertal nonadults. Since Gorjanović-Kramberger discovered Krapina over100 years ago, additional Neandertal fossils in Israel, France, Belgium, Italy and Uzbekistan have been recovered. Here the Krapina remains are compared to a large ontogenetic series of Neandertal adults, subadults, juveniles and infants (n = 41). Growth trajectories of Neandertal lower facial traits are used to assess the absolute growth of traits at Krapina. Principal components analyses, done separately for the lower maxilla and mandible, demonstrate some relationships between Krapina fossils and other Neandertals based on multiple traits. The results demonstrate that, compared to other Neandertals, Krapina nonadults exhibit long palates, and adults exhibit both tall and short mandibular symphyses, thickened mandibular corpora, short to mid-range ascending rami and relatively long mandibles. The alveolar process and lower piriform aperture are within the range of other Neandertals. The remains at Krapina record important growth signals characterizing late juvenile and subadult Neandertal ontogeny–life cycle stages that are largely absent from the Neandertal fossil record.

INTRODUCTION

The Krapina fossils represent an important range of variation for juveniles, subadults and adults that is typically lacking at most Upper Pleistocene sites *(1)*. One unfortunate aspect of the Krapina remains is the fragmentary nature of the fossils *(2)*. No complete crania exist, and most individuals are represented by isolated teeth, or teeth embedded within alveolar fragments. However, the ontogenetic variability of the facial fragments, which can be estimated from patterns of tooth eruption, is exceptionally preserved. Krapina provides researchers a unique opportunity to assess patterns of growth at a single Upper Pleistocene site.

Studies of Neandertals have primarily focused on adults *(3–9)*. The growth and development of Upper Pleistocene hominid remains has recently received attention because of the shear number of nonadults represented in this fossil record as well as the potential of nonadults to add important inference into understanding how adult forms arise. Tillier pioneered comparisons of nonadult Neandertals descriptively and analytically *(10–13)*. Minugh-Purvis added a much needed inventory of the Neandertal and early modern human nonadults to the literature *(14)*, as well as important analyses of the Neandertal remains *(15)*. Williams and colleagues assessed the Neandertal nonadults and adults under the rubric of heterochrony *(16–17)*, while Krovitz added a three-dimensional approach to understanding differences between Neandertals and modern humans *(18)*. Ponce de León and Zollikofer provided computer reconstructions of the most well preserved Neandertal nonadults *(19)*. Other researchers have explored Neandertal postcranial remains *(20)*, dental development *(21)*, mental foramen position *(22–25)* as well as descriptive morphology and dental traits *(26–30)*.

The Krapina assemblage has not been featured in all studies of Neandertal ontogeny probably due to the fragmentary nature of the remains, and the variability of individuals. Furthermore, the ontogenetic series represented at Krapina most likely spans several time intervals, and lacks unequivocal chronometric dates; excavation of the site in the late nineteenth/early twentieth centuries destroyed much of the contextual information forever. The potential temporal variation in the Neandertal sample is complicated further by the fact that the Krapina site most likely spans the last interglacial to the beginning of the last glacial time periods. Despite these caveats, most researchers consider Krapina as a single, albeit varied, population.

Patterns of growth and development evidenced at Krapina are difficult to assess without reference to a larger comparative sample. Modern humans may not be the most appropriate comparative sample for the Krapina remains because of marked cultural differences that tend to be expressed skeletally (e.g., dietary and behavioral differences contributing to craniofacial robustness). Furthermore, the selection of a reference sample of modern humans can greatly alter the results *(13–14)*. Fossils attributed to Middle Paleolithic sites (i.e., the Neandertals) are possibly the best sample to assess patterns of growth and development at Krapina due to presumed behavioral similarities. Since patterns of growth depend on estimates of age, and age in fossils is normally determined by patterns of dental eruption, teeth must be directly associated with the fossil remains to reliably estimate dental age. The Krapina sample largely comprises fragmentary individuals, so patterns of growth are necessarily confined to facial remains. The objective here is to compare the growth patterns manifested at Krapina to a large ontogenetic series of Neandertals.

METHODS AND MATERIALS

The Neandertal sample used in this analysis comprises 38 original fossils and three casts from a broad geographic range, including Belgium, Croatia, Czech Republic, France, Gibraltar, Hungary, Israel, Italy and Uzbekistan (Table 1). Life cycle stage was constructed solely on the basis of dental eruption. The neonate stage includes individuals with no dental elements erupted; infants include those individuals with all deciduous teeth erupted, but not M1; juveniles comprise individuals with M1 fully erupted, but not M2, subadults are individuals with M2 fully erupted, but not M3; and adults exhibit M3 at the occlusal plane.

In aging the Neandertal sample, the procedures and developmental profiles used to age modern humans were followed, although there is some evidence that Neandertals may have exhibited a more rapid dental eruption than that of modern *Homo sapiens (21, 30)*. Although the process of assigning minimum ages can be fraught with error, estimated age is absolutely necessary to understand

TABLE 1

List of 14 institutions visited and 41 fossils examined.

Location	Institution and Fossil Sample
Belgium	Institut Royal des Sciences Naturelles de Belgique (Spy 1, La Naulette)
	Diréction de l'Archéologie, Ministére de la Région Wallonne (Sclayn 3)
	Université de Liège (Engis 2)
Croatia	Croatian Natural History Museum (Krapina Maxillae B, C, D, E; Mandibles C, D, E, F, G, H, J; Rami 1and 4)
Czech	Moravske Museum (casts of Sipka and Ochoz)
England	British Natural History Museum (Forbes' Quarry, Tabun C1, Devil's Tower)
France	Musée de L'Homme (La Chapelle-aux-Saints, La Ferrassie, La Quina 5, Pech de l'Azé, Malarnaud)
	Musée des Antiquités Nationales-Saint Germain-en-Laye (La Quina 18)
	Muséum National de Préhistoire-Les Eyzies-de-Tayac (Roc de Marsal)
	Université de Poitiers (Châteauneuf-sur-Charente)
Hungary	Természettudományi Muzeum (Subalyuk 1 and 2)
Israel	Tel Aviv University (Amud 1 and 7, Kebara 2, cast of Teshik-Tash)
Italy	Museo Preistorico Ethnografico, 'Luigi Pigorini' (Guattari 1)
	Istituto di Paleontologia Umana (Circeo 2 and 3, Archi 1)

the growth of traits. Dental eruption patterns are believed to closely follow chronological age *(31–33)* because they are largely resistant to environmental insults (e.g., changes in nutrition, climate and disease) that affect the development of other bodily systems in humans. The same was probably true for Neandertals as daily incremental markings for a Tabun C1 first molar indicate that Neandertals and modern humans probably had similar rates of enamel formation *(34)*. Furthermore, Neandertal and modern human adult brain sizes overlap significantly. Smith *(33)* infers that adult brain size is highly correlated with age at M_1 eruption in anthropoid primates and she suggests a similar age at M1 eruption for Neandertals and modern humans on the basis of their great overlap in adult brain sizes. Indeed, the larger-brained Neandertals may have erupted their first molars slightly *later* than modern humans. Wolpoff *(30)* argues on the basis of dental wear that the third molar may have erupted earlier in Neandertals than in modern humans. In contrast to the idiosyncrasies of growth, estimated differences in timing are minor, however, and the schedule for modern human dental eruption was accepted as the best available timetable for Neandertals as well. Neandertals probably exhibited a maturation schedule similar to those observed among different populations of modern humans living today or in the recent past (cf. *35*).

Radiographs are available for many Neandertal juveniles (see *14* and references therein), but they were not available for all specimens observed. To be consistent, all individuals were aged without the use of radiographs, although the ages provided here, and those obtained from radiographs and calcification scores, are markedly consistent. In the present study, the dental stage of each tooth for each individual was scored, and the midpoint of the age range for each individual was then converted to a single year. Dental eruption scores were calculated for each deciduous and permanent tooth as follows: 0 = no crypt present; 1 = crypt present and crown calcified; 2 = tooth at or near alveolar margin; 3 = tooth one-third erupted; 4 = tooth two-thirds erupted; 5 = full eruption.

For the 21 Neandertal nonadults, modern human dental aging charts were used to assign ages to the nearest half year (Tables 2 and 3) (*31–32* and references therein). Ages for 21 Neandertal dental adults were approximated on the basis of tooth wear. A scoring system was developed for adults that consisted of seven stages. All dentally mature individuals were matched as closely as possible to these criteria: 18 years = all teeth at occlusal plane, teeth unworn; 20 years = minimal wear; 25 years = teeth moderately worn and some dentine ex-

TABLE 2

Permanent Dental Development Schedules for recent *Homo*.

Tooth	Age at eruption
1st Incisor (I1)	6.9 years
2nd Incisor (I2)	8 years
Canine (C)	10.5 years
1st Premolar (P3)	10.9 years
2nd Premolar (P4)	11.5 years
1st Molar (M1)	6.3 years
2nd Molar (M2)	12 years
3rd Molar (M3)	18 years

TABLE 3

Dental ages of the fossil sample (n = 41).

Life Cycle Stage	Fossil	Dental age in years
Neonate	Amud 7	0.5
Infants (pre-M1)	Subalyuk 2	2.5
	Pech de l'Azé	2.8
	Roc de Marsal	3
	Châteauneuf-sur-Charente	3
	Archi 1	3.5
	Engis 2	4.5
	Devil's Tower	5
Juveniles (pre-M2)	Krapina Maxilla B	6
	La Quina 18	7.5
	Krapina Maxilla C	9.5
	Teshik-Tash (cast)	9.5
	Krapina Mandible C	11
	Sclayn 3	11
	Sipka (cast)	11
Subadults (Pre-M3)	Krapina Mandible E	14
	Krapina Mandible D	15
	Krapina Mandible F	15
	Krapina Maxilla D	15.5
	Krapina Maxilla E	15.5
	Malarnaud	16
	La Naulette	17.5
Adults (post-M3)*	Krapina Mandible G	18
	Circeo 3	20
	Krapina Ramus 1	20
	Krapina Ramus 4	20
	La Quina 5	20
	Krapina Mandible J	25
	Subalyuk 1	25
	Ochoz (cast)	25
	Forbes' Quarry	25
	Amud 1	30
	Kebara 2	30
	Krapina Mandible H	30
	Spy 1	35
	La Ferrassie	35
	Guattari	40
	Circeo 2	40
	La Chapelle-aux-Saints	45

*Adult ages are based on a seriation of dental attrition and only represent approximate age intervals.

posed; 30 years = substantial tooth wear and dentine exposure, 35 years = teeth heavily worn with dentine exposed on every tooth; 40 years = no enamel present on teeth and moderate alveolar resorption; 45 years = substantial alveolar resorption from tooth loss. No Neandertal fossils over 50 years have been recovered *(36)*. Due to differences in diet and in rates of dental attrition, the scoring system for adults is intended to seriate individuals rather than to ascribe definitive chronological ages.

The Krapina sample

Only Krapina remains with associated dental elements were considered in this analysis. These include four maxillary remains (Maxillae B, C, D and E), seven mandibles (Mandibles C, D, E, F, G, H and J) and two ascending rami (Rami 1 and 4). These remains range from approximately 6 years old (Maxilla B) to over 30 years old (Mandible H), and are described in detail below, from youngest to oldest.

The Krapina Maxilla B maxillary fragment derives from a young juvenile (M^1 is only recently erupted) and is from an individual approximately 6 years of age. The maxilla is reconstructed close to the intermaxillary suture. The anterior dentition is small in size, and exhibits heavy wear (the dentine is exposed). The two deciduous molars are less worn, although dm^1 shows heavier wear than dm^2.

Krapina Maxilla C is approximately 9.5 years of age. Although much of the lower maxilla is preserved (right P^4 to left M^2), some of the anterior surface is eroded (including the canine jugum), exposing portions of the left and right canines, and dm^1/P^3 crypts. This maxillary fragment holds four teeth in situ. These include left dm^2, M^1 and M^2 (just beginning its descent), and right P^4 (only very partially erupted). Crypts are present for right P^3 and C, and left I^2, C and P^3. The deciduous m^2 is heavily worn, M^1 is only moderately worn, and M^2 is unworn.

Krapina Mandible C is approximately 11 years of age. This partial mandible consists of corpus and right ramus portions, and extends from left I_2 to right M_2. Crypts exist for left I_1, and right I_1 (right I_2, C and dm_1 crypts are not present due to damage to the alveolar bone). The lateral incisors, right dm_2, M_1 and M_2 are in situ. The entire inferior border of the corpus is preserved from the partial crypt of left dm_1 to the base of the right mandibular condyle. Mandible C is shallow, and the mandibular corpus and symphysis are short. The ascending ramus is gracile. The developing germ of P_4 can be seen under dm_2. Radovčić *et al.* (1988) suggest that ramus 67 is probably the antimere of mandible C. The occlusal surface of left I_2 (the only tooth in situ) exhibits heavy wear; a small amount of dentine is exposed. The deciduous m_2 is moderately worn, M_1 is less so. The second molar preserves its occlusal morphology. A very small crypt for M_3 exists; the developing M_3 is visible through a small postmortem foramen in the alveolar bone.

A number of subadults are included in the Krapina assemblage. The youngest of these is probably Krapina Mandible E, aged to approximately 14 years of age. This mandibular corpus fragment extends from right I_1 to left M_2. A large but undeveloped crypt is present for M_3. The mental region is tall (similar to mandible H), although not as tall as mandible G. Relative to its age, most of the teeth are only minimally worn. The occlusal surface of the incisors exhibits more pronounced wear, exposing some of the dentine. The premolars and M_2 exhibit extensive occlusal morphology. M_1 also preserves much of its original morphology, although the cusps have a polished texture.

Krapina Mandible F, aged to approximately 15 years of age, includes the mental region and a small portion of the left corpus to the partial crypt for M_2. The mental symphysis is short (similar to Mandible G). The inferior border is intact, but the alveolar margin is slightly damaged. Crypts exist for all teeth between and including right I_2 to left P_4. Partial crypts are present for left M_1 and M_2. P_4 is turned in a counterclockwise direction due to the tight spacing of P_3 and the canine. P_4 appears only very minimally worn, suggesting only a recent ante-mortem eruption.

Krapina Mandible D is aged to approximately 15 years of age, and extends from left I_2 to left M_2. The mental region is tall (similar to mandible H, although shorter). There is only minimal wear on the teeth.

Of similar dental age is Krapina Maxilla D. This small maxillary fragment extends from left P_3 to left M_2, although partial crypts for the left canine and I_2 are visible. The palate extends to the intermaxillary suture at M_1. The teeth (including M_1) exhibit minimal wear. The damaged anterior maxillary bone reveals the apices of the dental roots, although the apex for P_4 is missing.

Krapina Maxilla E is approximately 15.5 years old. This anterior half of this palate extends from right I^2 to left P^4. The occlusal surface of the incisors (particularly the central incisors) and the left canine exhibit dentine exposure and the anterior tooth row is worn to one functional level. There is much less wear on the premolars suggesting a recent eruption at the time of death.

The Krapina series also comprises a number of adults, the youngest of which may be Krapina Mandible G. This mandibular corpus fragment from a young adult, approximately 18 years of age, extends from the base of the right ascending ramus (including the gonial angle) to left P_4. Posterior to left P_4, the corpus largely is destroyed. Right M_1, M_2 and M_3 are preserved in situ and crypts for right P_4, P_3, C, I_2, I_1 and left I_1, I_2, C, P_3, P_4 are preserved. The mental symphysis is low in contrast to Mandible H. The Krapina assemblage also includes a number of isolated rami, such as Krapina Ramus 1. This left ramus consists of an almost complete mandibular condyle, coronoid process, mylohyoid groove and mandibular fossa. The third molar is preserved in the posterior margin of its crypt. Krapina Ramus 4 represents another isolated adult ramus. This complete right ramus preserves the mandibular condyle and the coronoid process lacks only its most superior aspect. The posterior inferior border of

TABLE 4

Nine linear distances used to reconstruct growth patterns of the lower face.

Face	Mandible
Biectomolare (breadth across the most lateral points on the alveolar margin of maxilla)	Mandibular Symphysis Height (infradentale-gnathion)
Palatal Length (prosthion-staphylion)	Mandibular Corpus Height (at mental foramen)
Maximum Nasal Aperture Breadth (bi-alare)	Mandibular Corpus Thickness (at mental foramen)
Palatal Breadth (bi-endomolare at widest point)	Mandibular Length (gonion-gnathion)
	Ascending Ramus Height (gonion to the most superior aspect of the mandibular condyle)

the ramus preserves a complete gonial angle, and a portion of the mandibular corpus to the root of M_3. The lateral one third of M_3 is missing. The root of M_3 is visible mesially. Both Krapina Ramus 1 and Ramus 4 are aged to approximately 20 years.

Krapina Mandible J represents the only virtually complete mandible, lacking only a portion of the right base of the ascending ramus just superior to gonial. The corpus of this mandible is thick and robust. Similar to mandible H, the mental symphysis is tall. The anterior dentition exhibits moderate to substantial wear and the enamel on the occlusal surface is destroyed; it was aged to approximately 25 years. The crowns of the molars and premolars are obliterated. The mandible lacks left M_3 and right P_3 (lost postmortem), and left P_3 (lost antemortem).

Another less well preserved adult mandible is Krapina Mandible H, aged to approximately 30 years. This adult mandibular corpus contains an entire tooth row (M_3 to M_3). The right corpus is destroyed just posterior to M_3. The inferior border of the corpus is well-preserved to M_2, although the left inferior border below M_2 is slightly more damaged than is the right one. The teeth (particularly the canines and incisors) exhibit substantial wear, and are reduced to one functional level. The occlusal surface is destroyed, revealing the dentine. The left P_3 is turned in a clockwise direction; the distal side of the tooth faces buccally. The mental region is thick and slopes posteroinferiorly from the alveolar bone to the base of an exceptionally tall mental symphysis.

Linear distances and preservation

The linear distances utilized in this study were chosen from the Chicago Standards (Buikstra and Ubelaker, 1994) and from Bass (1995) to represent the outer dimensions of the lower face (Table 4). Caliper measurements allow a greater number of individuals to be examined than 3-D digitization because interlandmark distances require a triangulation of coordinates, some of which may not be available for fragmentary remains. Even using linear distances, not every individual preserved all of the measurements of the lower face. Therefore, this database represents a sample based on availability and was subject to the completeness of the fossil record. Juveniles are better represented in the maxillary measurements, while more subadults and adults are better sampled for mandibular traits. In particular, two maxillae, B and C, and three mandibles, G, C and J, are better preserved than the other lower facial remains.

Growth trajectories

The only trait of the midface that was preserved in more than one individual is nasal breadth. Nasal breadth is compared to dental age to show how well the Krapina fossils compared to those of other Neandertals across postnatal ontogeny. Growth trajectories of Biectomolare and Palatal Length detail the outer dimensions of the lower maxilla in Krapina and other Neandertals. Mandibular growth is represented by ontogenetic changes in Mandibular Symphysis Height, Mandibular Corpus Breadth and Ascending Ramus Height. These traits of the mandible are well represented at Krapina, and provide a means to assess the overall dimensions of the lower jaw.

Principal Component Analysis

The Krapina remains, along with other Neandertals, are also examined within a multivariate framework. Principal components analysis is used assess the contribution of several traits simultaneously. The palate and mandible are analyzed separately each utilizing three traits. Palatal Length, Palatal Breadth and Biectomolare are compared across eleven individuals (including Maxillae B and C), whereas Mental Symphysis Height, Mandibular Corpus Height and Mandibular Length are compared to nineteen Neandertal fossils (including Mandibles C, G, and J).

RESULTS

Nasal breadth

The growth trajectory representing nasal breadth shows a monotonic increase in size across infants, juveniles, subadults and adults (n = 14). The Krapina sample includes one older juvenile, Maxilla C, and a subadult, Maxilla E, that help to bridge the gap between young infants and adults (Figure 1). Subalyuk 2 and Pech de L'Azé are the smallest and youngest of the individuals and exhibit virtually the same value for nasal breadth, while Roc de Marsal, which is slightly older in age exhibits a somewhat larger lower nasal aperture. Roc de Marsal is similar to Engis 2, followed by La Quina 18. Devil's Tower, while younger than La Quina 18 is markedly larger for this trait. Devil's Tower, aged to approximately 5 years old, is similar to Krapina Maxilla C at 9.5 years

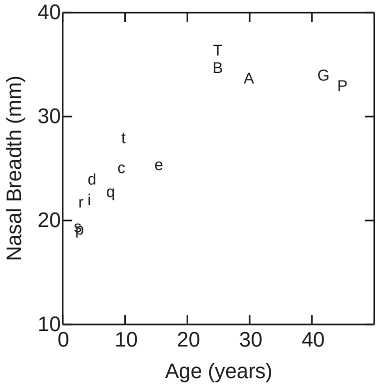

Figure 1. *Nasal Breadth compared to Age. Nonadults are given lower case and adults, upper case: c = Krapina Maxilla C; e = Krapina Maxilla E; t = Teshik-Tash; d = Devil's Tower; B = Forbes' Quarry; T = Tabun; p = Pech L'Azé; P = La Chapelle-aux-Saints; q = La Quina 18; i = Engis 2; s = Subalyuk 2; r = Roc de Marsal; G = Guattari; A = Amud 1.*

old and Maxilla E at 15.5 years of age. Nasal Breadth must have expanded rapidly during and after puberty in Neandertals. Maxilla E may be an outlier in this regard as it is similar in size to younger individuals, and dissimilar to adults. This comparison demonstrates the diversity of values for a given trait within the Neandertal sample and shows that the Krapina Neandertals can be characterized as falling on the lower end of the Neandertal distribution for breadth of the nasal aperture. Adult Neandertals all exhibit similar values for this trait.

Biectomolare

Sixteen Neandertal fossils are featured in a comparison of Biectomolare and age (Figure 2). Amud 1 exhibits the largest alveolar breadth, followed by La Ferrassie and La Quina 5, whereas Engis 2 exhibits the smallest value for this trait. The Krapina remains are well within the range of other Neandertals with respect to life cycle stage. Neandertal adults, such as La Chapelle-aux-Saints, La Ferrassie, Tabun C1 and Forbes' Quarry, are much larger than Guattari which exhibits substantial alveolar resorption. Krapina Maxilla C is smaller than similarly aged Teshik-Tash. Krapina Maxilla B is similar to Devil's Tower, but dissimilar to La Quina 18. Younger infants, such as Subalyuk 2, Pech de L'Azé and Roc de Marsal, exhibit diverse values for this trait. Like Nasal Breadth, the outer alveolar process must have expanded considerably during and after puberty to attain the sizes characterizing Neandertal adults.

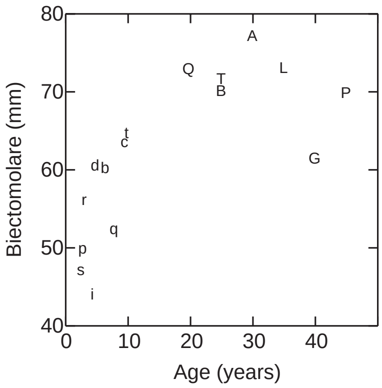

Figure 2. *Biectomolare compared to Age. Nonadults are given lower case and adults, upper case: b = Krapina Maxilla B; c = Krapina Maxilla C; r = Roc de Marsal; s = Subalyuk 2; p = Pech de L'Azé; i = Engis 2; q = La Quina 18; d = Devil's Tower; t = Teshik-Tash; T = Tabun C1; A = Amud 1; G = Guattari; L = La Ferrassie; Q = La Quina 5; B = Forbes' Quarry; P = La Chapelle-aux-Saints.*

Palatal Length

The Krapina sample exhibits long palates relative to other Neandertals of similar dental age (Figure 3). Tabun C1 exhibits the longest palate. Subalyuk 2 and Roc de Marsal exhibit similar values for palatal length and are considerably smaller than Pech de L'Azé. Krapina Maxilla B, although similar in age to Devil's Tower, is much larger for this trait, and far surpasses the value characterizing La Quina 18. The palatal length of Krapina Maxilla B approaches that of older Teshik-Tash. Meanwhile, Krapina Maxilla C, which is similar in age to Teshik-Tash, is notably longer; its palate is similar in length to Guattari and slightly longer than that of Amud 1, both adults. In contrast to Nasal Breadth and Biectomolare, adult values for the length of the palate may have been achieved during the juvenile phase of dental development, well before dental maturation.

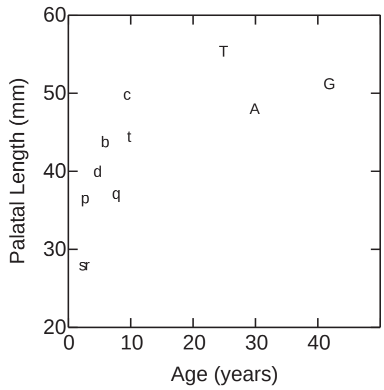

Figure 3. *Palatal Length compared to Age. Nonadults are given lower case and adults, upper case: b = Krapina Maxilla B; c = Krapina Maxilla C; r = Roc de Marsal; s = Subalyuk 2; p = Pech de L'Azé; q = La Quina 18; d = Devil's Tower; t = Teshik-Tash; T = Tabun C1; A = Amud 1; G = Guattari.*

Mandibular Symphysis Height

Mandibular symphysis height could be compared across a large number of individuals. The Krapina sample is within the range of values exhibited by Neandertals, but some individuals are tall, and others, shorter (Figure 4). Krapina Mandible J exhibits the tallest mental region of any of the Neandertals examined, followed closely by Kebara 2, Krapina Mandible H and Amud 1. Krapina Mandible E, a subadult, is already in the range of many Neandertal adults, such as Circeo 2 and 3, Subalyuk 1,

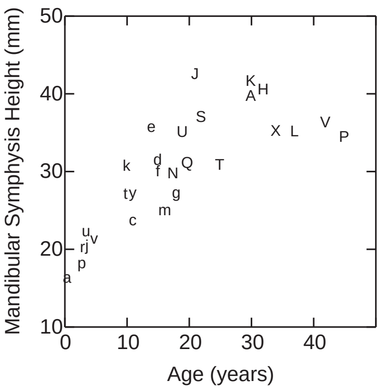

Figure 4. *Mandibular Symphysis Height compared to Age. Nonadults are given lower case and adults, upper case: c = Krapina Mandible C; d = Krapina Mandible D; e = Krapina Mandible E; f = Krapina Mandible F; g = Krapina Mandible G; H = Krapina Mandible H; J = Krapina Mandible J; t = Teshik-Tash; y = Sclayn; v = Devil's Tower; T = Tabun C1; L = La Ferrassie; p = Pech L'Azé; Q = Quina 5; P = La Chapelle-aux-Saints; q = La Quina 18; X = Spy 1; S = Subalyuk 1; m = Malarnaud; r = Roc de Marsal; N = Naulette; V = Circeo 2; U = Circeo 3; u = Archi 1; A = Amud 1; a = Amud 7; K = Kebara 2; j = Châteauneuf-sur-Clarente; k = Sipka.*

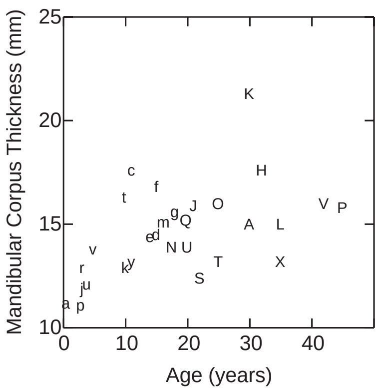

Figure 5. *Mandibular Corpus Thickness compared to Age. Nonadults are given lower case and adults, upper case: c = Krapina Mandible C= Krapina; d = Krapina Mandible D; e = Krapina Mandible E; f = Krapina Mandible F; g = Krapina Mandible G; H = Krapina Mandible H; J = Krapina Mandible J; t = Teshik-Tash; y = Sclayn; v = Devil's Tower; T = Tabun C1; L = La Ferrassie; p = Pech L'Azé; Q = Quina 5; P = La Chapelle-aux-Saints; X = Spy 1; m = Malarnaud; r = Roc de Marsal; N = Naulette; S = Subalyuk 1; V = Circeo 2; U = Circeo 3; u = Archi 1; A = Amud 1; K = Kebara 2; a = Amud 7; j = Châteauneuf-sur-Clarente; k = Sipka; O = Ochoz.*

Spy 1, La Ferrassie and La Chapelle-aux-Saints. Krapina Mandibles D and F, which are similar in age to Krapina Mandible E, exhibit much shorter mental symphyses, and are similar in size to some Neandertal adults, such as La Quina 5, Tabun C1, subadult Naulette, and the juvenile Sipka mandible. The mandibular symphysis of Krapina Mandible G, an adult, is much shorter than those of subadult Krapina Mandibles E, D, and F, and more similar to juveniles Sclayn 3 and Teshik-Tash. The mandibular symphysis of Krapina Mandible C is much shorter than similarly aged Scalyn 3, and is most similar to the Malarnaud mandible. Among Neandertal infants, Archi 1 exhibits the tallest and Pech de L'Azé the shortest mandibular symphysis. The Amud 7 infant exhibits a relatively tall mandibular symphysis given its neonatal age. The height of the mandibular symphysis seems to increase dramatically during the late juvenile phase in some Neandertals, whereas it increases less dramatically in others. This trend is clearly expressed at Krapina and may underlie patterns of sexual dimorphism and/or population differences.

Mandibular Corpus Thickness

Mandibular Corpus Thickness represents the most well preserved lower facial trait in this Neandertal sample (n = 29), and probably the entire hominid fossil record. Kebara 2 stands out as much thicker than the other mandibles. Among adults, Krapina mandible H could be characterized similarly albeit to a lesser extent (Figure 5). Krapina Mandible C exhibits an extraordinary thick mandibular corpus for its age, which may be partially related to the eruption of the permanent dentition in this juvenile. Krapina Mandible F, a subadult, also exhibits a particularly thickened mandibular corpus. Other Krapina mandibles may be similarly characterized with respect to subadult and adult Neandertals. For example, Krapina Mandible J is similar to Ochoz, Circeo 2, La Chapelle-aux-Saints and juvenile Teshik-Tash, while Krapina Mandible G is somewhat thinner, followed by La Quina 5, Amud 1, La Ferrassie and the subadult Malarnaud mandible. Krapina Mandibles D and E, both subadults, exhibit thicker mandibular corpora than several Neandertal adults such as Circeo 3, Tabun C1, Spy 1, and Subalyuk 1. Devil's Tower, Roc de Marsal, Sclayn 3, Sipka and Naulette are already within the range of several Neandertal adults. Neonate Amud 7 exhibits as broad a corpus as 3 year old Pech de L'Azé, although other three year olds, such as Châteauneuf-sur-Clarente and Archi 1 exhibit broader mandibular corpora. In general, Krapina mandibles tend to be thicker than most those of other Neandertals, regardless of life cycle stage.

Ascending Ramus Height

Ascending ramus height shows a rapid rate of growth as a function of age, and the Neandertal sample largely follows a monotonic increase from the neonatal period to the eruption of M_3 (Figure 6). Krapina adults approximate the middle of the range exhibited by other Neandertal adults. Krapina Mandible J and Krapina Ramus 4 exhibit slightly shorter rami than do Amud 1, Circeo 3, La Ferrassie, and are similar in size to Circeo 2. Krapina Ramus 1 is similar to La Quina 5, Tabun C1 and Kebara 2 in ramus height. Krapina Mandible C exhibits an exceptionally tall ramus, only slightly shorter than that of Kebara 2, and is much taller than that characterizing other juveniles, such as Teshik-Tash and Scalyn 3 and the subadult Malarnaud mandible. Younger individuals, such as Devil's Tower, Roc de Marsal, Pech de L'Azé and Amud 7 follow the growth trajectory of ramus height as a function of age.

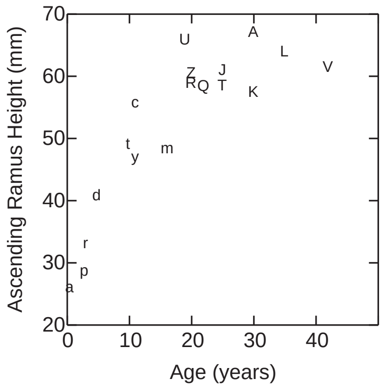

Figure 6. *Ascending Ramus Height compared to Age. Nonadults are given lower case and adults, upper case: c = Krapina Mandible C; J = Krapina Mandible J; R = Krapina Ramus 1; Z = Krapina Ramus 4; t = Teshik-Tash; y = Scalyn 3; d = Devil's Tower; T = Tabun C1; L = La Ferrassie; p = Pech L'Azé; Q = La Quina 5; m = Malarnaud; r = Roc de Marsal; V = Circeo 2; U = Circeo 3; A = Amud 1; K = Kebara 2; a = Amud 7.*

PCA of the palate

Three traits of the palate, Palatal Length and Breadth and Biectomolare, are compared in a principal components analysis of the lower maxilla (Figure 7). The first PC Axis, describing 85.2% of the variation, largely separates individuals on the basis of size as reflected in the component loadings associated with this vector (Table 5). This axis polarizes Amud 1 and Tabun C1, with particularly large alveolar breadths, from Subalyuk 2 with a short palate. PC Axis 1 has a strong ontogenetic signal, with the exception of Guattari which is closer to Krapina Maxilla C than it is to the other Neandertal adults. PC Axis 2, explaining 11.6% of the variance is largely a contrast vector separating individuals with palates longer than they are wide, such as Krapina Maxillae B and C, and Guattari, from individuals with short and broad palates, such as Roc de Marsal, Amud 1, Subalyuk 2 and Devil's Tower. In general, the Krapina maxillae can be described as relatively elongated and narrow with respect to those of other Neandertals.

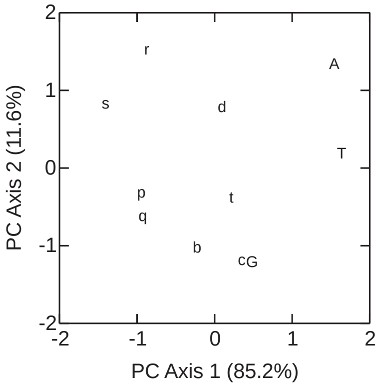

Figure 7. *Principal components analysis of the lower maxilla. Nonadults are given lower case and adults, upper case: b = Krapina Maxilla B; c = Krapina Maxilla C; r = Roc de Marsal; s = Subalyuk 2; p = Pech de L'Azé; q = La Quina 18; d = Devil's Tower; t = Teshik-Tash; T = Tabun C1; A = Amud 1; G = Guattari.*

TABLE 5

Component loadings for principal components analysis of the lower maxilla.

Traits	PC Axis 1	PC Axis 2
Palatal Length	0.879	–0.470
Palatal Breadth	0.922	0.344
Biectomolare	0.966	0.099

PCA of the mandible

The mandible is represented in a principal components analysis using three traits: Mandibular Symphysis Height, Mandibular Corpus Height and Mandibular Length (Figure 8). Like the PCA of the palate, the first PC Axis of the mandible (92.2% of the variance) polarizes large from small mandibles (Table 6). This size vector separates infants, such as Pech de L'Azé, Roc de Marsal, Archi 1 and Devil's Tower, from larger adults, including Kebara 2, Krapina Mandible J, Amud 1 and La Ferrassie. This axis also exhibits a strong ontogenetic signal, as all of the adults, including Krapina Mandible G, are separated from all of the nonadults. The second PC

TABLE 6

Component loadings for principal components analysis of the mandible.

Traits	PC Axis 1	PC Axis 2
Mandibular Symphysis Height	0.987	0.147
Mandibular Corpus Height	0.970	0.200
Mandibular Length	0.932	–0.363

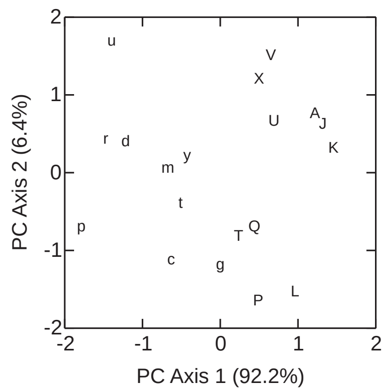

Figure 8. *Principal components analysis of the mandible. Nonadults are given lower case and adults, upper case: c = Krapina Mandible C; g = Krapina Mandible G; J = Krapina Mandible J; t = Teshik-Tash; y = Sclayn 3; d = Devil's Tower; T = Tabun C1; L = La Ferrassie; p = Pech L'Azé; Q = La Quina 5; P = La Chapelle--aux-Saints; X = Spy 1; m = Malarnaud; r = Roc de Marsal; V = Circeo 2; U = Circeo 3; u = Archi 1; A = Amud 1; K = Kebara 2.*

Axis, explaining 6.4% of the variance, separates individuals with relatively short mandibular symphyses and corpora (with respect to the length of their mandibles), such as Krapina Mandibles C and G, La Ferrassie and La Chapelle-aux-Saints, from individuals with relatively tall symphyses, such as Archi 1, Circeo 2, Spy 1, Amud 1, Circeo 3 and Krapina Mandible J.

DISCUSSION

A number of researchers have recently shown that many of the traits associated with adult Neandertals are manifested early in infancy *(18)*, perhaps even prenatally *(19)*. This accentuates the differences between Neandertals and modern humans and leads to labeling Neandertals as a separate species since their growth and development differs so radically from that of modern humans *(38)*. Other researchers have shown that Neandertals may have exhibited a much more rapid development compared to modern humans *(35)*. This adds to the modern human origins debate by further accentuating the differences between Middle Paleolithic humans and those deriving from Upper Paleolithic and modern contexts. This research shows that Neandertal growth is varied, even within a single site such as Krapina. Adults can also be characterized as differing radically from one another in just about every craniofacial feature imaginable. This should not be surprising as modern humans also differ considerably from one another. The idea that Neandertals are a monolithic group is simply incorrect.

A constellation of features are used to describe Neandertals and to set them apart from Upper Paleolithic and modern humans. Assuming that these features appeared early in ontogeny suggests a radical developmental shift may have occurred in modern human origins. This research shows, in contrast, that many traits that characterize adults appear during the juvenile and subadult periods of development. Traits of the mid-face and alveolus grow substantially during the subadult period, while the ramus and mandibular symphysis grow in a gradual fashion, from infancy to adulthood in Neandertals. Length of the palate, in contrast, tends to grow more rapidly during infancy among Neandertals such that adult values are obtained during the juvenile period. The mandibular corpus tends to swell during the eruption of the permanent teeth and for this reason shows much less of a relationship with ontogeny. The extended life history of Neandertals is clearly evident from the large brain size characterizing adults *(33)*. Neandertals most likely had similar rates of enamel accumulation and patterns of dental eruption compared to modern humans *(34)*. However, modern humans do stand apart from their Pleistocene counterparts as the growth and development of Upper Paleolithic humans is more similar to that of Neandertals than it is to Holocene *Homo (14)*. It is the fossils from Krapina, among others that allow for generalizations to be made. The Krapina fossils in particular greatly augment the sparse number of older juveniles and subadults comprising the Neandertal fossil record.

CONCLUSIONS

With respect to other Neandertals, the Krapina fossils can be characterized as exhibiting particularly elongated and narrow palates, both tall and short mandibular symphyses and thickened mandibular corpora. The Krapina fossils fall well within the ontogenetic series for many traits including breadth of the piriform aperture, ramus height, and width of the alveolus. These fossils exhibit important growth signals that are essential to adequately infer patterns of growth and development in archaic humans, including the variation that accompanies such ontogenetic reconstructions.

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