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RESEARCH ARTICLE

External auditory exostoses among western Eurasian late Middle and Late Pleistocene humans

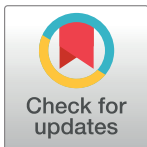
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Abstract

External auditory exostoses (EAE) have been noted among the Neandertals and a few other Pleistocene humans, but until recently they have been discussed primarily as minor pathological lesions with possible auditory consequences. An assessment of available western Eurasian late Middle and Late Pleistocene human temporal bones with sufficiently preserved auditory canals ($n = 77$) provides modest levels of EAE among late Middle Pleistocene archaic humans ($\approx 20\%$) and early modern humans (Middle Paleolithic: $\approx 25\%$; Early/Mid Upper Paleolithic: 20.8%; Late Upper Paleolithic: 9.5%). The Neandertals, however, exhibit an exceptionally high level of EAE (56.5%; 47.8% if two anomalous cases are considered normal). The levels of EAE for the early modern humans are well within recent human ranges of variation, frequencies which are low for equatorial inland and high latitude samples but occasionally higher elsewhere. The Early/Mid Upper Paleolithic frequency is nonetheless high for a high latitude sample under interpleniglacial conditions. Given the strong etiological and environmental associations of EAE development with exposure to cold water and/or damp wind chill, the high frequency of EAE among the Neandertals implies frequent aquatic resource exploitation, more frequent than the archeological and stable isotopic evidence for Middle Paleolithic/Neandertal littoral and freshwater resource foraging implies. As such, the Neandertal data parallel a similar pattern evident in eastern Eurasian archaic humans. Yet, factors in addition to cold water/wind exposure may well have contributed to their high EAE frequencies.

Introduction

In his classic monograph on the Neandertal skeleton from the Bouffia Bonneval in La Chapelle-aux-Saints, Corrèze, France, Marcellin Boule [1] noted the presence of bony growths (exostoses) in the auditory canals (“Ces orifices présentent quelques exostoses. L’orifice gauche est rétréci vers son milieu par des productions osseuses qui lui donnent une forme en sablier” ([1] p. 152). He did not comment further on them, but since that time the presence of external

auditory exostoses has been noted in ten Middle Pleistocene humans [2–5], three additional Neandertals [6,7], three eastern Eurasian later archaic human [5], a few eastern early modern humans [5,8], and in one western Upper Paleolithic modern human [9]. Given that the frequencies of these bony growths across recent human populations appear to reflect primarily patterns of environmental exposure (plus inherited predispositions to form them) [10], an assessment of them among western Eurasian Late Pleistocene humans may provide insights into the morbidities and (by extension) behaviors of late archaic to early modern humans in the region.

External auditory exostoses (EAE; torus acusticus) are dense bony growths protruding into the external auditory canal. They are frequently observed clinically in modern humans, often in the context of aquatic sports (hence references to their presence as “swimmer’s ear” or “surfer’s ear”). First documented more than a century ago clinically [11,12], their distributions across human populations have been considered anthropologically since the 1930s [13–17], being employed as one of suite of discrete cranial traits for population affinity studies. However, their distribution among later Holocene humans has been shown to vary latitudinally and to correlate with habitual exposure to cold water [5,18–21]. In particular, clinical and bioarcheological observations indicate that they are principally due to an environmental irritation of the mucoperiosteum of the external auditory canal (see [10,18,22]). As first noted by Van Gilse [23] and Harrison [24], the most frequently observed irritant is cold water, in the context of cold water sports [25–31] or foraging [19,21,32–34]. Clinical reports also show that ears exposed to a combination of water and cold air, as represented by wind chill, are more likely to develop EAE and at a faster rate [25,28,35].

However, EAE may occur in a variety of contexts, given sufficient inflammation of the soft tissue lining of the auditory canal. They are often benign but can lead to cerumen impaction and conductive hearing loss [24,26,36–39] (see [7]). They are also frequently more common in males [14,18,21,40–44] (but see [32]), probably relating more to sex differences in activities than differential susceptibility [18,45].

Given this framework, observations on EAE among the available western Eurasian Middle and Upper Paleolithic humans, including both presence/absence and degree of formation, are provided. The primary samples of concern are Middle Paleolithic Neandertals and Upper Paleolithic modern humans, but observations are also included for the few sufficiently intact late Middle Pleistocene archaic humans and early Late Pleistocene (Middle Paleolithic) modern humans.

Materials and methods

External auditory exostoses are identified as growths into the auditory canal from its squamous and/or tympanic portions [16,22,46]. They are usually rounded protrusions and may occur as single or multiple growths. They normally do not involve or development from the tympanosquamous or tympanomastoid sutures; such sutural protrusions are osteomata, or benign neoplasms, which normally occur laterally within the meatus, are less frequent and are often solitary [22,46].

The EAE were scored using the four part ordinal scale of Cooper et al. [26], Crowe et al. [41] and Villotte et al. [32] (see also [16]). Grade 0 indicates the absence of EAE, Grade 1 indicates small mildly protruding single or multiple exostoses (<1/3 of the canal), and Grade 2 reflects one or more large EAE projecting well into the auditory canal (1/3–2/3 of the canal). Grade 3 indicates a meatus which is largely or completely blocked by exostosis growth (>2/3 of the canal). Given the irregularities of EAE growths and their variable positions with the canal versus at the lateral margin, these grade distinctions are inevitably subjective but

nonetheless serve to categorize EAE severity. For crania that provide bilateral observations of EAE, the EAE is scored as “present” if an exostosis is evident on at least one side. In the comparisons by grade, each side is scored as 0.5 in the sample summaries by grade if the two meatus have different grades of EAE formation.

A number of the Pleistocene tympanic bones are thickened at their lateral margins, especially where the inferior tympanic crest meets the porus, and some of them exhibit small nubbins of bone along the lateral tympanic margin. These changes are not considered to be part of the EAE, which consist of bony growths into the meatus.

The paleontological observations (S1 Table) have been made whenever possible visually on twenty-nine original Pleistocene specimens, by us ($n = 24$) and/or the paleontologists who have commented on presence/absence of EAE in individual specimens ($n = 5$). When high quality (resin) casts are available, they have been employed. Otherwise, the additional observations are based on high resolution digital scans of the temporal bones or detailed photographs that provide a clear view directly into the auditory meatus. For the lost Předmostí crania, observations are based on the sufficiently clear photographs in Velemínská and Brůžek [47]. The photographs and scans employed are available either as referenced in S1 Table or through the authors. The resin casts indicated are available in the Departments of Anthropology of either Washington University in Saint Louis or the University of Iowa, Iowa City. The observations of EAE presence/absence and degree of development, made on original fossil specimens by other scholars, are presented and referenced in S1 Table. The 24 original fossil specimens, on which we scored EAE and which are listed in S1 Table, are curated in the institutions provided in Table 1. Except for the Cro-Magnon and Pataud remains in the Musée de l'Homme (Colhelper request 46669), permissions were obtained through correspondence with the person(s) responsible for the fossil remains (Table 1).

The principal methodological limit of the study is the difficulty in scoring early EAE (see [30,32]), and the relative subjectivity in the ordinal scoring an irregular continuous trait (i.e. the relative size of an exostosis into the auditory canal), especially considering the diversity of the material used (original fossils, casts, scans, photographs). In order to circumvent this issue, the grade scores allotted in the study were checked by all authors and discussed before reaching a final agreement. Moreover, if the EAE appears intermediate between two grades, it was counted conservatively as the lower grade. Thus, even if our study cannot be considered as fully reproducible by other researchers, we consider that this would produce only minor differences (i.e. differences between two adjacent grades for few individuals). For example, the differences between the Neandertal sample and the more recent ones are evident for each grade of EAE (see below), making it unlikely that small changes in some individual scores would alter the clear trend illustrated here.

The primary samples include Neandertals and earlier and later Upper Paleolithic modern humans (S1 Table). The Neandertal sample ($n = 23$) derives from Europe and southwest Asia, from early Marine Isotope Stage (MIS) 5 to the middle of MIS 3. The Upper Paleolithic modern humans are separated into an MIS 3 Early/Mid Upper Paleolithic (E/MUP) sample (83.3% MUP) ($n = 24$) and an MIS 2 Late Upper Paleolithic one ($n = 21$); the former sample is entirely European, but the latter one includes one southwest Asian specimen (Ohalo 2). Additional data are included for small samples of late Middle Pleistocene (MIS 6) archaic humans ($n = 5$) and an early Late Pleistocene (MIS 5) Middle Paleolithic modern humans (MPMH; $n = 4$).

The three primary samples are all male biased (for the sexable specimens) (Table 2), although they are not different from each other in sex proportions ($\chi^2 p = 0.976$). They are also biased towards young adults plus older adolescents versus older adults (Table 2), as are Late Pleistocene mortality profiles in general [48]. However, the three samples are not significantly different from each other if the adolescents and young adults are pooled ($\chi^2 p = 0.941$).

Table 1. Locations of original fossil human specimens observed by us for the scoring of external auditory exostoses.

<i>Specimen</i>	<i>Curating Institution</i>	<i>Location</i>	<i>Permission</i>
Shanidar 1, 5	Iraq Museum	Baghdad, Iraq	Isa Salman
Bausu da Ture 2	Musée d'Archéologie Nationale	Saint-Germain-en-Laye, France	C. Schwab
Cro-Magnon 1, 2	Musée de l'Homme	Paris, France	D. Grimaud-Hervé, V. Laborde
Dolní Věstonice 13 to 16	Archeologický ústav AV CR	Dolní Věstonice, Czech Republic	J. Svoboda, S. Sázlová
Muierii 2	Institutul de Speologie "Emil Racoviță"	Bucharest, Romania	S. Constantin
Oase 2	Institutul de Speologie "Emil Racoviță"	Bucharest, Romania	S. Constantin
Pataud 1	Musée de l'Homme	Paris, France	D. Grimaud-Hervé, V. Laborde
Pavlov 1	Archeologický ústav AV CR	Dolní Věstonice, Czech Republic	J. Svoboda, S. Sázlová
Sunghir 1	Laboratory of Anthropological Reconstruction, Russian Academy of Sciences	Moscow, Russia	T.S. Balueva
Bichon 1	Laténium: Parc et Musée d'Archéologie de Neuchâtel	Hauterive, Switzerland	M.-A. Kayser, D. Ramseyer, F.-X. Chauvières
Chancelade 1	Musée d'Art et d'Archéologie du Périgord	Périgueux, France	V. Merlin-Anglade
Iboussières A	Musée d'Archéologie Tricastine, Service Régional d'Archéologie Rhône-Alpes	Saint-Paul-Trois-Châteaux, France	M. Lert
Lafaye 1	Musée d'Histoire Naturelle Victor Brun	Montauban, France	A. Berteret
Laugerie Basse 4	Musée d'Archéologie Nationale	Saint-Germain-en-Laye, France	C. Schwab
La Peyrat 5	Musée Labenche	Brive-la-Gaillarde, France	L. Michelin
Rochereil 1	Institut de Paléontologie Humaine	Paris, France	H. de Lumley
St. Germain-la-Rivière 4	Musée National de Préhistoire	Les Eyzies, France	J.-J. Cleyet-Merle
San Teodoro 1, 2	Museo Geologico Gemmellaro	Palermo, Italy	C. Di Patti

<https://doi.org/10.1371/journal.pone.0220464.t001>

Therefore, although EAE, as a degenerative process, generally increases in frequency and/or severity with age and/or exposure [30,34,43,49–51], the age distributions should not affect the comparisons across these Late Pleistocene samples.

To provide a recent human reference framework, presence/absence data are presented for 120 recent human samples (S2 Table). As originally proposed by Kennedy [18], they are separated by latitude into those <30°, those between 30° and 45°, and those >45° (north and

Table 2. Sex and age distributions for the late Middle and late Pleistocene samples.

	Late Middle Pleistocene	Neandertal	Mid. Paleol. Mod. Humans	Early/Mid Upper Paleol.	Late Upper Paleolithic
Sex ¹					
Male	0	8	1	12	12
Female	0	4	1	7	7
Indeterminate	5	11	2	5	2
Age					
Adol./YA ²	1	14	4	15	11
Old Adult	0	7	0	6	6
Adult	4	2	0	3	4

¹ The male and female counts include both pelvically and craniofacially sexed remains.

² Given that the adolescent remains are all late adolescent and routinely considered as adult, and that the included cranial/temporal remains from the large Krapina sample cannot be aged to adolescent versus young adult, the adolescent and young adult (YA) samples are pooled in the counts.

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south). In addition, within each latitudinal range and given the predilection for EAE to form when the auditory canal is exposed to cold water, they are separated into “wet” versus “dry” samples (S2 Table); the former samples are coastal/riverine/lacustrine ones with known or likely exposure to water, and the latter are inland ones with little aquatic exposure. It is fully recognized that these “wet” and “dry” categories are approximate, given the archeological contexts of many of the samples. However, separating the samples along these lines provides additional detail for the recent human framework, given the differences in EAE frequencies evident between adjacent coastal and inland samples [19,33,34]; minor resorting of the samples into the “wet” versus “dry” categories is unlikely to alter substantially the distributions of presence/absence of EAE. Moreover, they are provided as a framework for evaluating the later Pleistocene sample frequencies and not as a reassessment of recent human EAE epidemiology. Only samples with $n > 30$ are included, and pooled national, large island and immigrant samples are excluded. Given the absence of male versus female and age data for many of the samples, sexes are pooled where frequencies are provided separately by sex and all are considered as “adult” unless otherwise indicated. There are 30 low-latitude, 15 mid-latitude and 16 high-latitude samples assigned to the ‘wet’ group, and 22 low-latitude, 19 mid-latitude and 18 high-latitude samples assigned to the ‘dry’ group (S2 Table).

In addition, to provide a framework for EAE severity distributions, the fossil scores are compared to the available grade data for a smaller number (14) of recent human samples [19,21,32,42,51,52], also divided into “wet” ($n = 10$) and “dry” ($n = 4$) categories with the frequencies pooled within each category. The resultant frequencies are grade 0: 98.2%, grade 1: 1.8%, grade 2: 0.0% and grade 3: 0.0% for the pooled “dry” sample; they are grade 0: 76.6%, grade 1: 16.6%, grade 2: 4.5% and grade 3: 2.4% for the pooled “wet” sample (S3 Table).

In the statistical comparisons, exact Chi-square and binomial p-values were computed using StatXact 4.0.1 [53], and Wilcoxon / Mann-Whitney p-values were determined using NCCS 11.0.19 [54] for the latitudinal distributions of the samples. Binomial 95% confidence intervals for the fossil sample EAE percentages derive from the online calculator of Soper [55].

Results

Presence/Absence of external auditory exostoses

All of the later Pleistocene western Eurasian samples provide at least one individual with clearly developed external auditory exostoses. In the two smaller samples, the late Middle Pleistocene archaic human and the Middle Paleolithic modern human ones, one individual in each sample provides a modest (grade 1) EAE, providing sample frequencies of 20% and 25% (despite large 95% confidence intervals (CIs) of 5.1%– 71.6% for the late Middle Pleistocene sample and 6.3%– 80.6% for the Middle Paleolithic modern human one). If the values have any meaning given the large CIs, they suggest frequencies among the higher of the recent human middle latitude and low latitude “wet” samples (Fig 1).

The larger Upper Paleolithic samples provide frequencies with smaller 95% CIs, ones of 20.8% (CI: 4.8%– 48.5%) for the E/MUP sample and 9.5% (CI: 1.2%– 30.4%) for the LUP sample (Fig 1). Their 95% CIs span two-thirds of the recent human samples, but the mean values (especially the higher E/MUP one) are above most of the high latitude percentages and above all of the low latitude “dry” ones; yet they are well within the other recent human ranges of frequencies. The E/MUP frequency is nonetheless at or above the interquartile ranges of all of the recent human distributions except for the middle latitude “wet” sample.

In contrast, the Neandertal sample, with a mean frequency of 56.5% (CI: 34.5%– 76.8%) is well above all except two low latitude “wet” samples, one each from the Canary Islands and the southern Brazilian coast (S2 Table). The next closest are a middle latitude “wet” sample from

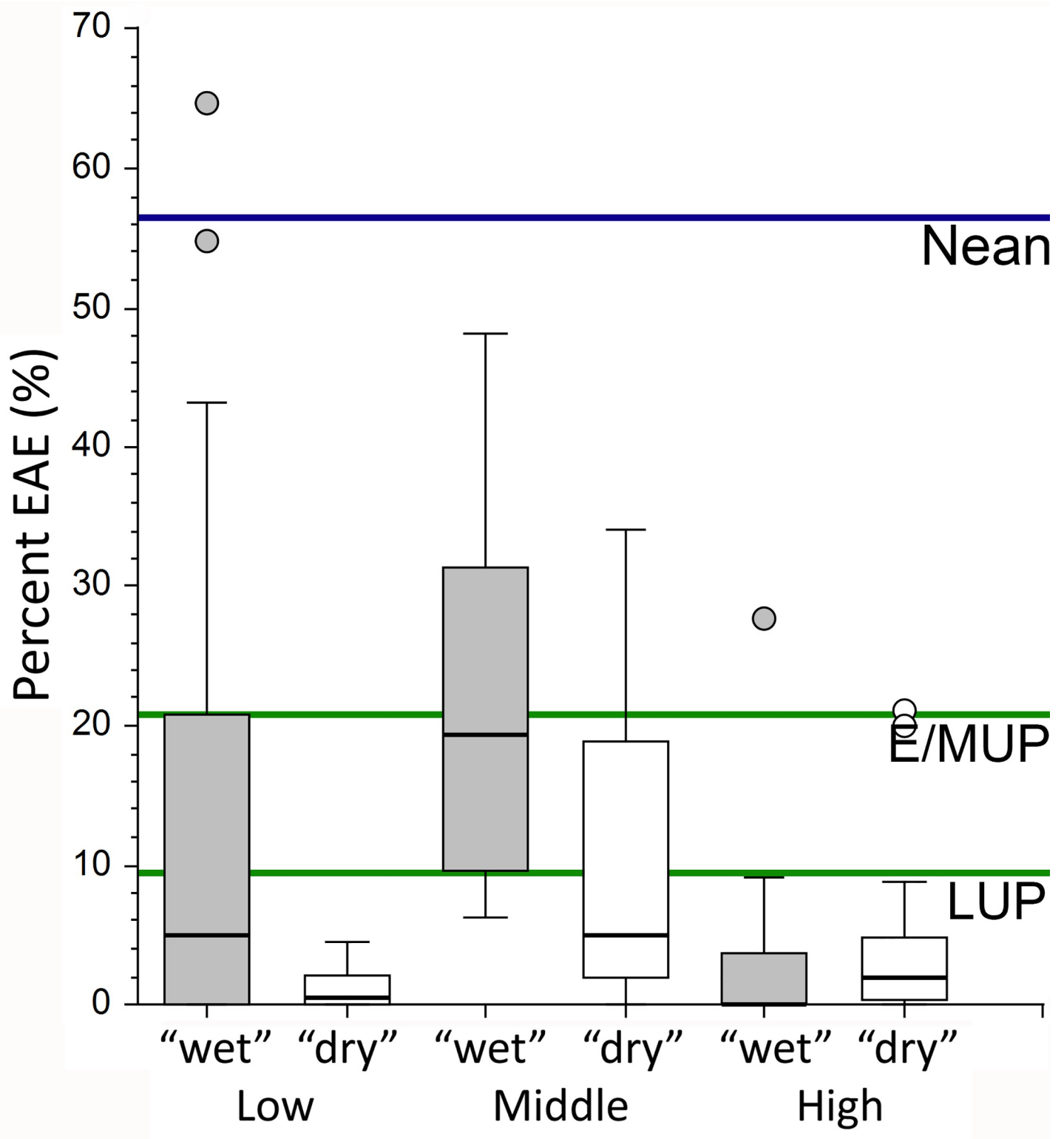


Fig 1. Percent presence of external auditory exostoses (EAE) in samples of Neandertals, Early/Mid Upper Paleolithic modern humans (E/MUP), Late Upper Paleolithic modern humans (LUP), and latitudinal samples of recent humans. The recent humans are divided into low (<30°), middle (35° - 40°) and high (>40°) latitude samples, and each one is then separated into coastal/riverine/lacustrine (“wet”) and inland (“dry”) samples; see S2 Table for justification and individual sample percentages. The 95% CIs are for 34.5%– 76.8% for the Neandertals, 4.8%– 48.5% for the E/MUP sample, and 1.2%– 30.4% for the LUP sample.

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eastern Turkey and low latitude “wet” one from the southern Brazilian coast [31,51,56]. Even its lower 95% CI limit is above the frequencies of all except six recent human samples (four low latitude “wet” ones and two middle latitude “wet” ones (S2 Table)), or 5.0% of the 120 recent human samples. The Neandertal frequency is significantly above the LUP one and its lower CI limit only overlaps the upper CI limit of the E/MUP sample modestly.

Distributions of external auditory exostosis severity

The presence/absence frequencies for EAE are reflected as well in the distributions of the severity grades across the samples (Fig 2). The EAE for the recent human “dry” and E/MUP samples are restricted to grade 1, larger numbers of individuals (but still a modest number) with grades 2 and 3 are present in the recent “wet” samples. There is also a grade 2 in the LUP sample for one cranium, Iboussières A (Fig 3), and the grade 1 value represents one cranium, Laugerie Basse 4. In contrast, the Neandertal sample includes a specimen with bilateral grade 3 (Shanidar 1 [7]; Fig 4), three with grade 2 on the one sufficiently preserved side (Krapina 39.1, Spy 1 and Tabun 1), and one with grade 2 unilaterally (La Chapelle-aux-Saints 1) (Fig 4). Therefore, 19.6% of the Neandertal sample presents grades 2 or 3, with an additional 37.0% exhibiting grade 1. Among the recent human samples providing grade frequencies, only the Körtik Tepe sample comes close to the Neandertal grade distribution, with a grade 2 plus 3 frequency of 13.5% and a grade 1 frequency of 34.6% (S3 Table).

Age and sex external auditory exostosis differences

Even though there is little difference across the primary samples in terms of younger versus older individuals, it is possible that some of the more developed Neandertal EAE is partially age-related. The only Late Pleistocene individual with grade 3 exostoses, Shanidar 1, is an older adult based on dental wear and pubic symphyseal morphology [6]. The older La Chapelle-aux-Saints 1, based on its auricular surface [57], exhibits grade 2 EAE on one side, but grade 1 in the other meatus. The other individuals with grade 2 exostoses, Krapina 39.1, Spy 1, Tabun 1 and Iboussières A, are all younger adults, the latter three based on dental wear and the first on the age distribution of the Krapina sample [58].

It is possible to evaluate the degree of sexual difference in EAE presence for the Neandertal and E/MUP samples, despite the small sample sizes per sex; the other samples are too small or have too few EAE cases to provide a reliable assessment. In the Neandertal sample, for the 12 individuals for which sex can be assigned or estimated, EAE occurs in 60.0% of the males ($n = 8$) and 75% of the females ($n = 4$). In the 19 sexable E/MUP specimens, EAE are present in 16.7% of males ($n = 12$) and 28.6% of females ($n = 7$). The females have modestly higher frequencies in both samples, but in neither case are the sex frequencies significantly different from 0.5 (binomial $p = 0.453$ and 0.453 respectively). The pattern of higher male frequencies in many recent human samples therefore does not appear to be present among these Late Pleistocene humans.

Discussion

Cold water and external auditory exostoses

In her 1986 analysis of global distributions of EAE, Kennedy [18] argued that EAE should be most frequent among middle latitude populations, given the presumed avoidance of cold water at high latitudes and the insufficient stimulation of low latitude warmer water to produce EAE. Subsequent research (Fig 1) has confirmed her hypothesis for high latitude samples, but it has provided a more mixed perspective for middle and low latitudes. Middle latitude samples

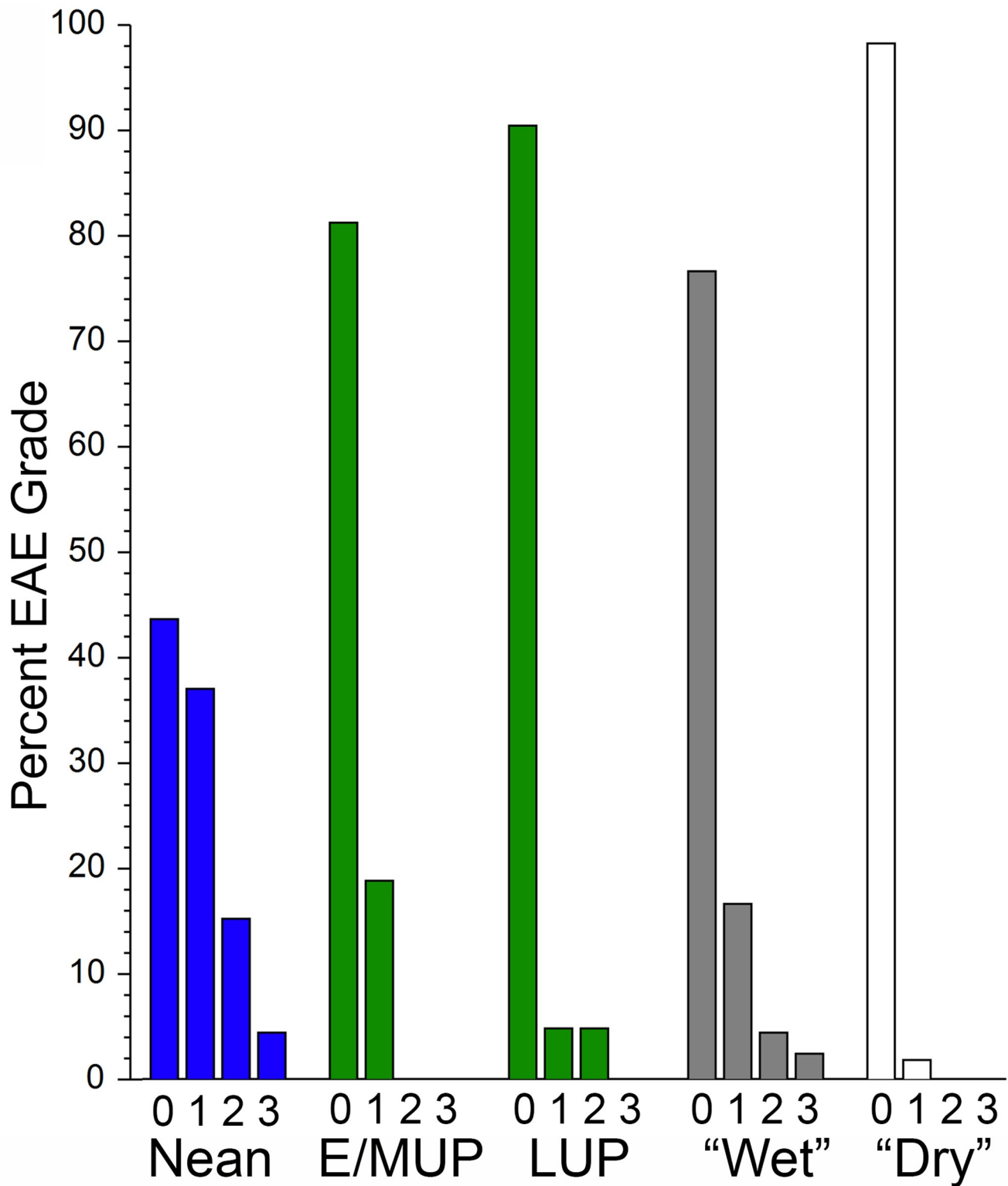


Fig 2. Distributions of external auditory exostosis (EAE) grades for samples of Neandertals, Early/Mid Upper Paleolithic modern humans (E/MUP), Late Upper Paleolithic modern humans (LUP), and coastal/riverine/lacustrine (“wet”) versus inland (“dry”) samples of recent humans. The paleontological data are in [S1 Table](#), and the recent human data are in [S3 Table](#).

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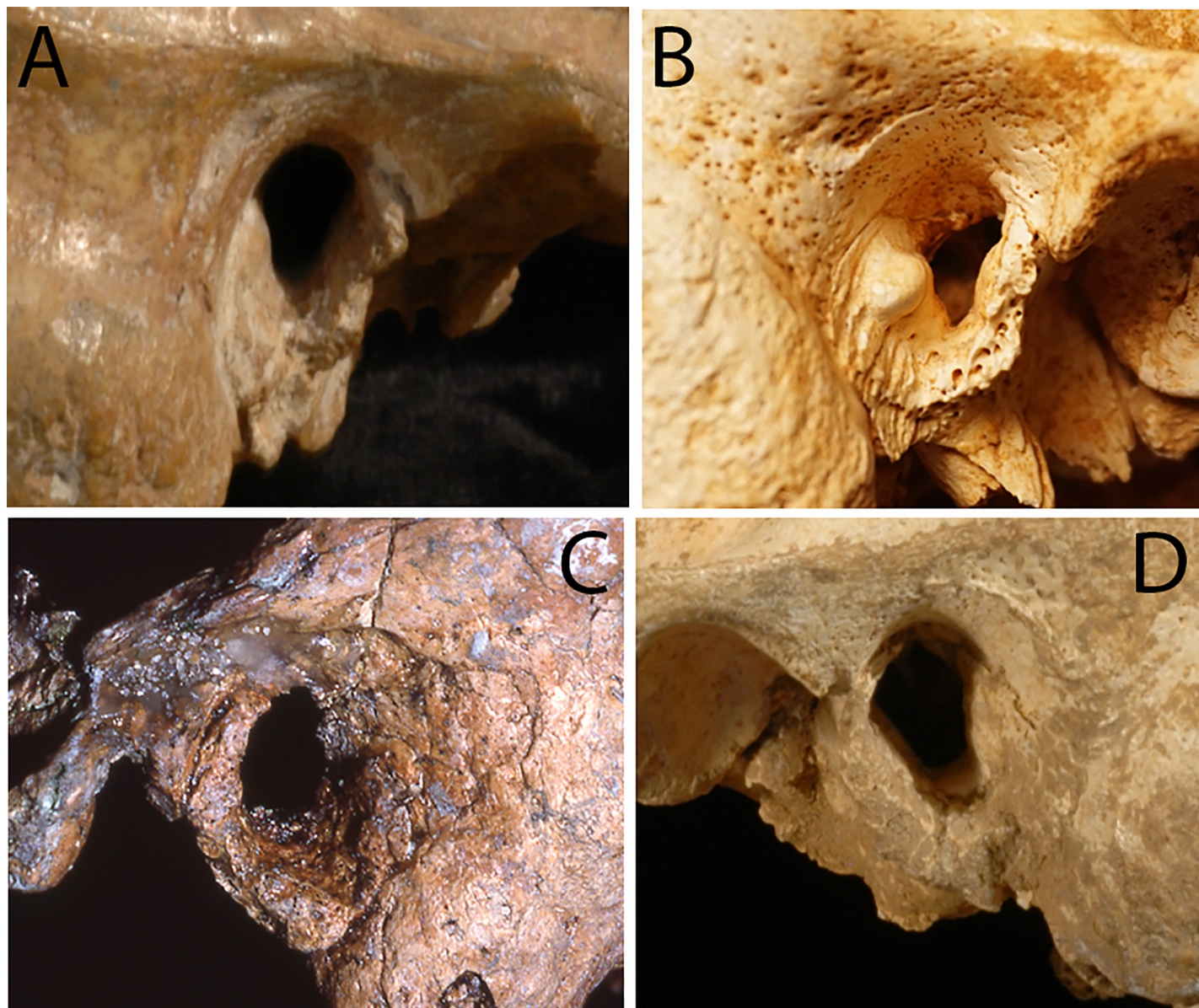


Fig 3. Examples of external auditory exostoses (EAE) among early modern human specimens. A: E/MUP Cioclovina 1 right (grade 1); B: LUP Iboussières A right (grade 2); C: MPMH Skhul 6 left (grade 1); D: E/MUP Oase 2 left (grade 1). Not to scale. Photos: A, C and D: E. Trinkaus; B: M. Samsel.

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do generally have higher frequencies of EAE. Yet, in both the middle latitude and equatorial regions, coastal/riverine/lacustrine samples exhibit consistently higher frequencies of EAE overall (Fig 1), and regional studies of archeological samples with more terrestrial versus aquatic resource exploitation provide similar contrasts [19,32–34]. Moreover, it has become evident that cephalic immersion in cold water is not necessary to promote EAE environmentally, and that exposure to cold and damp (maritime) winds is sufficient [31,33].

Therefore, as discussed above (see esp. [10]), there is a strong, but not deterministic, relationship between cold water exposure (especially when associated with wind chill) and the prevalence of EAE (see also [23]). It remains possible that there is an inherited predisposition to developing EAE. It is reflected in differential vasodilation susceptibility of the auditory canal

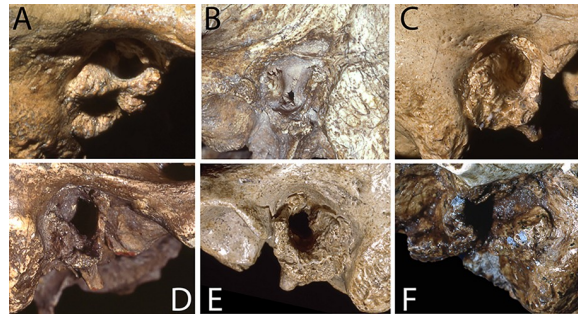


Fig 4. Examples of external auditory exostoses (EAE) among Neandertal specimens. A: Shanidar 1 right (grade 3); B: La Chapelle-aux-Saints 1 left (grade 2); C: Krapina 3 right (grade 1); D: Spy 1 right (grade 2); Krapina 39.1 left (grade 2); Tabun 1 left (grade 2). Not to scale. Photos: A, B, C, E and F: E. Trinkaus; D: H. Rougier.

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to cold water irrigation, found experimentally in rodents [25] and in the varying degrees of individual EAE development evident in aquatic sport samples subjected to similar environmental conditions [26,28,50,59]. Yet, it is unknown whether there are populational differences in EAE susceptibility, and it appears likely that recent human population differences in EAE are primarily related to environment and behavior.

In this context, the frequency of EAE in the LUP sample is unexceptional relative to recent humans. It is low relative to the middle latitude “wet” samples, and moderately high for the low latitude “dry” and the high latitude samples. Among the sites, Moča, Oberkassel and Zlatý kůn are modestly north of 45° N (all <52° N), and the southern French, northern Italian and Swiss sites distribute around the 45° N latitude. Only the Sicilian site of San Teodoro and the Israeli one of Ohalo II are below 40°. It nonetheless remains unclear how much colder these sites may have been during MIS 2 [60]. The only coastal sites are Arene Candide and San Teodoro, but Ohalo II is on the edge of the Sea of Galilee and Moča 1 was found in Danube River gravels. There is abundant evidence for aquatic resource exploitation at Ohalo II [61], but coastal resources seem not to have been particularly exploited at San Teodoro [62]; it is unclear to what extent marine resources were utilized at Arene Candide (besides shells for beads) [63,64], and no relevant data exist for Moča [65]. The two specimens with EAE, Iboussières A and Laugerie Basse 4, derive from inland sites, although the former site is not far from the Rhône and the latter one overlooks the Vézère. It is therefore difficult to assess whether the low frequency of EAE in the LUP sample is related to the generally higher latitudes of most of the specimens, even though its overall EAE frequency is unexceptional for many recent human samples.

The E/MUP sample provides a higher overall frequency of EAE, albeit all grade 1. The sites yielding observable auditory meatus range from 44° to 56° N, and the five specimens with EAE on at least one side span this geographic range (from Cioclovina 1 at 45° to Sunghir 1 at 56°). Of these specimens, only one (Bausu da Ture 2) can be considered coastal [66], even at MIS 3 lower sea levels, and all of them should have experienced temperatures substantially below the later Holocene ones of the recent human samples [67]. The E/MUP sample should therefore be compared primarily to the recent human high latitude ones; its EAE frequency of 20.8% is slightly below the maximum values of 21.1% and 27.7% for the high latitude “dry” and “wet” groups, but substantially above their means of 3.6% and 3.4% and medians of 0.0% and 2.0%. Even the lower limit of its 95% CI (4.8%) exceeds the means of these recent human groups.

If the E/MUP EAE frequency is moderately high for the relevant recent human environmental group, the Neandertal one is exceptional. As noted, only six of the recent human

samples have frequencies above its 95% CI lower limit, and only two “wet” samples provide frequencies similar to the Neandertal one. The Neandertal sample spans middle to high latitudes, from 33° to 50°. Only three of the specimens can be considered as coastal (Forbes’ Quarry 1, Guattari 1 and Tabun 1) [68–70], although Amud 1 was close to the Sea of Galilee [71], and many of the other Neandertals were adjacent to or near streams or modest rivers. They range paleoclimatically from temperate zones in early MIS 5 Europe (Krapina) and MIS 5 to 3 southwest Asia (Amud, Shanidar and Tabun) plus extreme southwestern Europe (Forbes’ Quarry), to substantially colder MIS 3 climates at La Chapelle-aux-Saints, La Ferrassie, La Quina, and Spy (see [60] and [72] for general western Eurasian Late Pleistocene climatic patterns). It is therefore difficult to correlate the high frequency of EAE (including their higher grades of EAE) among these Neandertals with climatic factors.

Evidence for aquatic resource exploitation among these Neandertals varies considerably, in part due to older excavations (and hence partial recovery of small fish bones) at a number of the sites yielding human remains with sufficiently intact temporal bones. There is skeletal and residue analysis evidence for the exploitation of fish among Neandertals in western Europe [73–76], cases of littoral mollusk exploitation along the Mediterranean and coastal Iberia [68,77,78], marine mammal use in southern Iberia [79], and crustacean use in western Iberia [80] (see also [81]). In addition, there are probable water lily starch grains from the Spy Neandertal dental calculus [82]. Yet, stable isotope analysis of 29 Neandertals (albeit all inland, but including the two Spy adults with their EAE) suggests little exploitation of freshwater vertebrate resources [83–85].

Although there is no evidence of littoral resource exploitation in the region of Tabun Cave, there is evidence of mollusk use further north on the eastern Mediterranean coast [77,86]. Therefore, it may be reasonable to attribute the advanced (grade 2) EAE of Tabun 1 to her coastal environment, and it is possible that some of the inland Neandertals with EAE were engaged in freshwater aquatic resource foraging. It nonetheless appears difficult to ascribe their overall high frequency of EAE solely to maritime/riverine/lacustrine environments.

In addition, although most of the EAE present in Neandertal auditory canals are characteristic rounded, knob-like growths (Fig 4; S1 Table), three of the auditory canals that exhibit growths are more irregular in their extra bone formations. These meatus include Amud 1, La Ferrassie 1 left, and La Quina 27. There is also extra posterior canal thickening of the Krapina 3 and 39.1 and the Tabun 1 canals (Fig 4). These variations in the growths raise the question as to whether all of the Neandertal EAE represent responses to cold water irritation of the canal, and whether some of them might be due to alternative etiologies. Yet, even if Amud 1 and La Quina 27 are not included among those with EAE (the La Ferrassie 1 right porus exhibits a more typical EAE growth and hence is scored as having EAE), the Neandertal frequency remains high, at 47.8% (CI: 26.8% - 69.4%).

Archaic versus Early modern human external auditory exostoses

There is therefore a substantial decrease in EAE frequency from Neandertals to early modern humans in western Eurasia, with a possible decrease from the earlier to later Upper Paleolithic modern humans. The Upper Paleolithic samples are nonetheless not significantly different from each other despite a lower frequency in the LUP sample (see 95% CIs above); the Neandertal and LUP frequencies are significantly different, and the Neandertal and E/MUP frequencies are modestly less distinct (if not significantly different).

The E/MUP sample is significantly higher in latitude than especially the Neandertal one (Wilcoxon $p < 0.001$), but they do not differ meaningfully in terms of maritime/riverine/lacustrine versus inland contexts (3 of 23 versus 1 of 24; $\chi^2 p = 0.238$). The LUP sample is

intermediate in its latitudinal distribution (χ^2 $p = 0.849$ versus the Neandertal sample), it has the highest number of specimens with maritime/riverine/lacustrine contexts (9 of 21), but it also has the lowest EAE frequency. It is therefore possible that factors other than cold water exposure influenced the differences between the Neandertals and the Upper Paleolithic modern human samples. This inference is supported by the apparent increase in aquatic resource exploitation through the Late Pleistocene, of both littoral and riverine/lacustrine resources [77,87–90].

At the same time, the Middle and Late Pleistocene archaic humans from eastern Eurasia also exhibit a high frequency of EAE. The eastern Middle Pleistocene crania provide a frequency equivalent to the Neandertal one (53.3%, $n = 15$); the addition of the three early Late Pleistocene archaic humans raises the frequency to 68.8% ($n = 18$) [5]. Yet, the early modern human remains from eastern Eurasia also exhibit an elevated EAE frequency (58.3%, $n = 12$). Although some of the eastern Eurasian specimens are associated with aquatic contexts, that alone does not appear sufficient to explain their elevated EAE frequency [5].

These data from western and eastern Eurasia therefore suggest that etiological factors in addition to cold water irritation of the auditory canal may have contributed to their elevated frequency of this condition. Could general meatal sanitary conditions be responsible for the additional growths? Could many of these individuals have had a predisposition to develop exostoses in the auditory canal, at higher frequencies than among most recent human populations? Or are the external auditory exostoses indicating a pattern of aquatic resource foraging prior to the Upper Paleolithic that is poorly documented in the Eurasian archeological and stable isotopic records?

Conclusions

Building on the previously scattered observations of external auditory exostoses among the Neandertals, it appears that there was a very high frequency of EAE among these late archaic humans, yet unexceptional levels of them (relative to most recent human samples) among western Eurasian early modern humans. The frequency of EAE for the E/MUP sample is nonetheless moderately high for a sample that should have been paleoclimatically similar to recent human high latitude ($>45^\circ$) populations. It remains likely that the high level of EAE among the Neandertals, and the E/MUP samples given its paleoenvironmental context, is due in part to the exploitation of aquatic resources. However, the Neandertal frequency is at the upper limits of recent human population values and is matched only by those who experienced cold water maritime climates. It is therefore likely that, as with eastern Eurasian later archaic humans, multiple factors were involved in their abundance of EAE.

Supporting information

S1 Table. External auditory exostoses (EAE) for western Eurasian late Middle and Late Pleistocene human remains.

(PDF)

S2 Table. Frequencies of external auditory exostosis (EAE) presence in samples of recent humans.

(PDF)

S3 Table. Distributions of external auditory exostosis grades among the recent human samples providing grades of severity.

(PDF)

SI File. Acknowledgments; supplementary information references.
(PDF)

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External auditory exostoses among western Eurasian late Middle and Late Pleistocene humans

Supplementary Information

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S1 Later Pleistocene and Recent Human Auditory Exostoses

Table S1. External auditory exostoses (EAE) for western Eurasian late Middle and Late Pleistocene human remains.

	<i>Lat</i>	<i>Side</i>	<i>Age</i> ¹	<i>Sex</i> ²	<i>EAM exostoses</i>	<i>Grade</i>	<i>Source</i> ³	<i>Scorer</i> ⁴	<i>Ref</i> ⁵
Late Middle Pleistocene									
Biache 1	50°	lt	YA	--	absent, thick tympanic with external growths	0	original [1]	[1]	[1]
Biache 2	50°	lt	A	--	absent, thick tympanic	0	cast	ET	[2]
La Chaise-BD 7	46°	rt	A	--	posterior and inferior growths on tympanic	1	original [3]	[3], ET	[3]
Ehringsdorf 9	51°	lt	A	--	absent, very thick tympanic posteroinferior	0	photo [4]	ET	[4]
Reilingen 1	49°	rt	A	--	absent, moderately thick tympanic walls	0	cast	ET	[5]
Neandertals									
Amud 1	33°	rt	YA	M	small posterior growth (inferior tympanic	1	cast; photo	ET	[6]
		lt			missing)	1			
La Chapelle-aux-Saints 1 ⁶	45°	rt	OA	M	large filling posterior with internal	1	original [8];	ET	[7,8]
		lt			thickening and additional bone	2			
La Ferrassie 1	45°	rt	OA	M	medium knob anterior, lateral knob posterior	1	[9]; photos	ET	[9]
		lt			medium posterior and large anterolateral	1			
					growths; closed down to very small canal				
					medially				
					small-to-medium growth mid-posterior				
					internally; small knob anteroinferior				
					spicules and growths in from tympanic				
					around anterior and inferior porus				

Table S1 (cont.)

	<i>Lat</i>	<i>Side</i>	<i>Age</i> ¹	<i>Sex</i> ²	<i>EAM exostoses</i>	<i>Grade</i>	<i>Source</i> ³	<i>Scorer</i> ⁴	<i>Ref</i> ⁵
La Ferrassie 2	45°	rt	OA	F	absent	0	photos	ET	[9]
Forbes' Quarry 1	36°	rt	OA	--	irregular margins but no apparent growths	0	photos	ET	[10]
Guattari 1	41°	rt	OA	(M)	very small superior and anteroinferior growths, otherwise round	1	photos	ET	[11]
		lt			small superior and small posterior growths, interior rounded ones	1			
Krapina 3 ⁷	46°	rt	Adol/YA	(F)	distinct rounded posterior middle protrusion	1	photo; cast	ET	[12,13]
Krapina 5	46°	rt	Adol/YA	(M)	absent	0	cast	ET	[12,13]
Krapina 10	46°	lt	Adol/YA	--	absent	0	photo	ET	[12,13]
Krapina 38.1	46°	rt	Adol/YA	--	absent, thick tympanic	0	photo	ET	[12,13]
Krapina 38.7	46°	rt	Adol/YA	--	absent, thick tympanic, possible posterosuperior new bone	0	photo	ET	[12,13]
Krapina 38.16	46°	rt	Adol/YA	--	medium posterosuperior knob	1	photo	ET	[12,13]
Krapina 39.1	46°	lt	Adol/YA	--	medium anterosuperior growth; large knob posteriorly on thick tympanic	2	original [3]; photo	[3], ET	[12,13]
La Quina 5	45°	rt	YA	--	absent	0	original	[14], ET	[14]
		lt			absent	0	[14]; photo; cast		
La Quina 10	45°	lt	A	--	absent, thickening of tympanic anterior and posterior	0	photo	ET	[14]
La Quina 27	45°	rt	A	--	broad irregular growth across inferior porus from anteroinferior to posterior, superoposterior spicules, thick tympanic	1	photos	ET	[14]
Saccopastore 1	42°	lt	YA	(F)	small knob from posteroinferior tympanic	1	photos	ET	[15]
Saccopastore 2	42°	rt	YA	(M)	absent, thick tympanic	0	photos	ET	[15]
Shanidar 1 ⁶	37°	rt	OA	M	large and bridging exostosis across porus	3	original;	ET	[17]
		lt			large posterior growth, superior and inferior internal knobs	3	[16,17]; photos		
Shanidar 5	37°	lt	OA	(M)	absent, thick tympanic	0	original; cast; photos	ET	[17]
Spy 1 (I)	50°	rt	YA	--	large posterior superior and inferior growths	2	photo	ET	[18,19]

Table S1 (cont.)

	<i>Lat</i>	<i>Side</i>	<i>Age</i> ¹	<i>Sex</i> ²	<i>EAM exostoses</i>	<i>Grade</i>	<i>Source</i> ³	<i>Scorer</i> ⁴	<i>Ref</i> ⁵
Spy 10 (II)	50°	rt lt	YA	--	modest posterior interior knob in broad posterior swelling small posterior knob with posteroinferior thick tympanic	1 1	photos	ET	[18,19]
Tabun 1	33°	rt	YA	F	small rounded posterior growth, large anterosuperior growth	2	photos	ET, SV	[20,21]
Middle Paleolithic Modern Humans									
Qafzeh 6	33°	rt lt	YA	--	absent thin growth along posterosuperior porus	0 0	cast; photo	ET	[22,23]
Qafzeh 9	33°	rt	Adol	F	absent	0	cast; photo	ET	[22,23]
Skhul 5	33°	rt lt	YA	M	absent (anterior tympanic missing) absent	0 0	cast; photo	ET	[20,24]
Skhul 6	33°	lt	YA	--	growths inferiorly and around posterior tympanic	1	photo	ET, SV	[20,24]
Early/Mid Upper Paleolithic									
Bausu da Ture 2	44°	lt	YA	M	absent	0	original [25]	SV	[25]
Brno 2	49°	lt	OA	(M)	absent, thick tympanic	0	photo	ET	[26,27]
Cioclovina 1	45°	rt lt	YA	(M)	clear rounded posterosuperior protrusion clear rounded swelling along posterior canal	1 1	photos	ET	[28,29]
Cro-Magnon 1	45°	rt	OA	M	absent	0	original	SV, ET	[30-32]
Cro-Magnon 2	45°	lt	OA	(F)	absent	0	original	SV, ET	[30-32]
Dolní Věstonice 3	49°	rt lt	YA	F	absent absent	0 0	photos	ET	[33]
Dolní Věstonice 13	49°	rt lt	YA	M	absent, thick tympanic absent, thick tympanic	0 0	original	ET	[33]
Dolní Věstonice 14	49°	lt	Adol	M	absent	0	original	ET	[33]
Dolní Věstonice 15	49°	rt lt	YA	M	absent absent	0 0	original	ET	[33]
Dolní Věstonice 16	49°	rt lt	OA	M	absent absent	0 0	original	ET	[33]

Table S1 (cont.)

	<i>Lat</i>	<i>Side</i>	<i>Age</i> ¹	<i>Sex</i> ²	<i>EAM exostoses</i>	<i>Grade</i>	<i>Source</i> ³	<i>Scorer</i> ⁴	<i>Ref</i> ⁵
Mladeč 1	50°	lt	Adol	(F)	absent	0	photo	ET	[34]
Mladeč 2	50°	lt	Adol	(F)	inferior, inferoposterior and superoposterior protruding bony spicules	1	photo	ET	[34]
Mladeč 5	50°	rt	A	(M)	absent	0	photo	ET	[34]
Muierii 2	45°	lt	A	--	absent	0	original	ET	[35]
Oase 2	45°	lt	Adol	--	small rounded posterior growth, beginning of a small anteroinferior growth	1	original	ET	[36]
Pataud 1	45°	rt	YA	F	absent	0	original	SV, ET	[37]
		lt			tiny knob posteriorly within canal	0			
Pavlov 1	49°	rt	OA	(M)	very small swelling inferoanterior	0	original	ET	[33]
		lt			absent	0			
Předmostí 1	49°	rt	Adol	--	absent	0	photo [39]	ET, SV	[38,39]
Předmostí 4	49°	rt	YA	F	inferior growths closing one-third of porus	1	photo [39]	ET, SV	[38,39]
Předmostí 9	49°	rt	YA	M	absent	0	photo [39]	ET, SV	[38,39]
Předmostí 10	49°	rt	YA	F	small posterosuperior growths	0	photo [39]	ET, SV	[38,39]
Sunghir 1	56°	rt	OA	M	small irregular growths anteroinferior; swelling with fine protrusions mid-posterior, closing of the inferior porus	1	original; photos	ET	[40]
		lt			absent	0			
Sunghir 5	56°	lt	A	--	absent	0	photo	ET	[40]
Vilhonneur 1	46°	rt	Adol	--	absent	0	photo [41]	ET	[41]
Late Upper Paleolithic									
Arene Candide 2	44°	rt	YA	M	absent	0	scan [42]	VS	[43]
		lt			absent	0			
Arene Candide 4	44°	lt	YA	M	absent	0	scan [44]	VS	[43]
Arene Candide 5	44°	rt	YA	M	absent	0	scan [45]	VS	[43]
Arene Candide 12	44°	rt	A	M	absent	0	scan [46]	VS	[43]
		lt				0			
Arene Candide 16	44°	rt	Adol	M	absent	0	scan [47]	VS	[43]
		lt			absent	0			

Table S1 (cont.)

	<i>Lat</i>	<i>Side</i>	<i>Age</i> ¹	<i>Sex</i> ²	<i>EAM exostoses</i>	<i>Grade</i>	<i>Source</i> ³	<i>Scorer</i> ⁴	<i>Ref</i> ⁵
Bichon 1	47°	rt	YA	M	absent	0	original	MS	[48]
		lt			absent	0			
Chancelade 1	45°	rt	OA	(F)	absent	0	original	MS	[49,50]
		lt			absent	0			
Iboussières A ⁶	44°	rt	YA	M	large rounded growth mid-posterior, with smaller swelling medial of it and extending to mid-inferior; low swelling along anterior tympanic	2	original; [51]	MS, SV	[52,53]
		lt			bilobular growths mid-posterior and posteroinferior, broad swelling anteroinferior, and small swelling posterosuperior	2			
Lafaye (Bruniquel) 1	44°	rt	YA	F	absent	0	original	MS	[54,55]
		lt			absent	0			
Laugerie Basse 4	45°	rt	OA	(M)	small swelling along mid-posterior porus	1	original	MS	[55,56]
		lt			diffuse growth along inferior meatus	1			
Moča 1	48°	rt	OA	(F)	tiny smooth swelling along superior tympanic margin	0	[57];	ET, SV	[57]
		lt			tiny smooth swelling along superior tympanic margin	0	photos		
Oberkassel 1	51°	rt	OA	M	absent	0	CT scan	ET	[58]
		lt			absent	0			
Oberkassel 2	51°	rt	YA	F	absent	0	CT scan	ET	[58]
		lt			absent	0			
Ohalo 2	33°	lt	OA	M	absent	0	cast	ET	[59,60]
Le Peyrat 5	45°	rt	A	M	absent	0	original	MS	[61,62]
Rochereil 1	45°	rt	OA	--	absent	0	original	MS	[63]
		lt			absent	0			
St Germain-la-Rivière 4	45°	rt	YA	F	absent	0	original	MS	[64]
		lt			absent	0			
San Teodoro 1	38°	lt	YA	F	absent, small lateral tympanic nubbins	0	scan; original	MS, VS	[65,66]

Table S1 (cont.)

	<i>Lat</i>	<i>Side</i>	<i>Age</i> ¹	<i>Sex</i> ²	<i>EAM exostoses</i>	<i>Grade</i>	<i>Source</i> ³	<i>Scorer</i> ⁴	<i>Ref</i> ⁵
San Teodoro 2	38°	rt	A	--	absent	0	original;	MS, VS	[65,66]
		lt			absent	0	scan		
Villabruna 1	46°	lt	YA	M	absent	0	scan; photo	VS, ET	[67]
Zlatý kůň 1	50°	rt	A	(F)	absent	0	photo [19]	ET	[68]

¹ The age categories are approximate, and the crania are divided into later adolescents (Adol), younger adults less than ≈ 40 years (YA) and older adults greater than ≈ 40 years. The adolescents are all ≥ 15 years and are considered adolescent based largely on the incomplete eruption of the M3s. A number of them (e.g., Dolní Věstonice 14, Mladeč 1 and 2) are routinely considered as though they are mature, and it is unclear whether the Krapina remains are late adolescent or young adult (see note 7).

² Sex indications without parentheses are based on pelvic remains. Those designations placed within parentheses are based on combinations of craniofacial rugosity and body size, as available. The latter designations are less certain for the Neandertals in particular, although those for individuals from the sites of Krapina, Saccopastore and Shanidar are based on ranges of variation with each site sample.

³ The source indicates the previous publication of EAE presence/absence for the specimen (for the few that have been published), and whether the observations were made by one of us on the original fossil, a high quality (resin) cast of the fossil, high quality photograph(s), CT scans, and/or digital surface scans. “Original” followed by a reference indicates an observation on the original specimen by the author of the publication. For photographic scoring, the reference is provided if a published photograph was employed; otherwise the photograph(s) are by the authors. In some cases (e.g., the Shanidar and Sunghir remains), the original observations on EAE were made on the original specimens, but the grade scoring was done from photographs and/or casts.

⁴ The initials of the author(s) primarily scoring the grade of EAE are provided, and all cases were double checked by the others. In cases of published EAE observations, the original comments have been translated into grade scores, resulting in a reference and an author’s initials. MS: M. Samsel; ET: E. Trinkaus; SV: S. Villotte; VS: personal communication from V.S. Sparacello.

⁵ Reference providing basic context and description of the skeletal remains.

⁶ The La Chapelle-aux-Saints 1, Shanidar 1 and Iboussières A partial skeletons each exhibits a suite of pathological lesions, including trauma, enthesopathies, and osteoarthritis [17,51,69,70]. Although their bilateral EAE were noted and briefly described (but not given grades) by Boule [7], Trinkaus [17] and Aymard [51] respectively (but see [71] for Shanidar 1), none of their EAE appear to be related to the other lesions on the remains, most of which can be attributed to the rigors of a Pleistocene foraging existence. Only the DISH of Shanidar 1 [72] and the femoral diaphyseal lesions of Iboussières A [51] are unusual for a Pleistocene human, and they are unlikely to have affected their auditory canals.

⁷ None of the included Krapina crania (Krapina 3, 5 and 10) or isolated temporal bones (Krapina 38.# and 39.1) preserve reliable adolescent versus adult or younger versus older adult age indicators. However, all of these temporal bones appear fully mature [73] and the associated dental remains provide an age range from juvenile to young adult [74]. These Krapina specimens are therefore considered as adolescent/young adult.

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Supplementary Information

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S1 Later Pleistocene and Recent Human Auditory Exostoses

Table S2. Frequencies (%) of external auditory exostosis (EAE) presence in samples of recent humans.

The samples are grouped into low (<30°), middle (30° - 45°) and high (>45°) latitude samples following Kennedy [75], and within each, into “wet” (coastal/riverine/lacustrine) and “dry” (inland with little or no aquatic exploitation).

The samples only include adults and later adolescents (>≈15 years). Male and female samples are combined, given that the data are not available by sex for a substantial number of the recent human samples. It is nonetheless recognized that a number of studies (e.g., [76-81]) have found substantial differences in the male versus female frequencies, with the males often having the higher incidence. Small (n < 30) samples are not included.

In the allocation of the samples into the “wet” versus “dry” categories, several factors were employed. In cases in which the authors have provided explicit contrasts between coastal/riverine versus terrestrial residence/occupation/resource exploitation (e.g., [78-80,82-84]), their divisions have been followed. For inland localities with little or no evidence of aquatic resource exploitation, the samples have been considered “dry.” Yet, inland (riverine) sites are considered “wet” where there is evidence of aquatic resource exploitation (e.g., Iron Gates Mesolithic sites, Indian Knoll). Coastal samples, even if there is no associated evidence for the exploitation of littoral resources, have been placed in the “wet” category, given the effects of general maritime exposure and associated wind chill [80,85]. Pooled samples based on national boundaries, immigrant groups, and pooled samples from very large islands with both coastal and inland areas are not included. It is fully recognized that some of the samples considered to be “wet” or “dry” could be placed in the other category. However, such resorting is not likely to substantially alter the “wet”/“dry” distributions within each of the latitudinal zones.

It is also recognized that the latitudinal zones, with cut-offs at 30° and 45°, are partially arbitrary, especially given variation in sea temperatures at a given latitude due to major oceanic currents. Those samples which fall close to a latitudinal boundary (e.g., Chinook, Arikara) have been placed in the higher latitude sample. These comments only serve to reinforce that such a global analysis, in contrast to detailed ones within regions, primarily serve to highlight overall patterns. They are employed here, not to resolve the detailed patterns of EAE incidence across recent human samples, but to provide a framework for evaluating the western Eurasian later Pleistocene distributions.

<i>Site</i>	<i>Frequency (%)</i>	<i>n</i>	<i>Reference</i>
Low Latitude (<30°) “dry”			n = 22
Australia-North	1.5	172	[75]
Australia-Central	3.2	127	[75]

<i>Site</i>	<i>Frequency (%)</i>	<i>n</i>	<i>Reference</i>
Australia-Queensland	4.5	110	[75]
Australia-North Territory	0.7	132	[75]
Australia-North Queensland	0.0	54	[75]
Punjab	0.0	53	[75]
Lachish, Israel	0.0	695	[75]
Egypt XX Dynasty	1.8	379	[75]
Egypt XXI Dynasty	2.7	75	[75]
Egypt Pre-dynastic	0.0	60	[75]
Egypt Middle Kingdom	0.0	182	[75]
Egypt Late period Giza	0.0	50	[75]
Canary Islands Interior	0.0	45	[84]
Canary Islands Highlands	0.9	226	[86]
Nubia-Jebel Moya	0.0	32	[75]
Nubia-Historic	1.2	431	[87]
Nubia-Kerma	0.4	224	[87]
Ashanti	0.0	56	[75]
Khoisan	0.0	123	[88]
Ayala, Ecuador	2.9	103	[75]
Botocudo, Brazil	2.5	40	[80]
Cerca Grande, Brazil	2.0	50	[80]
Low Latitude (<30°) “wet”			n = 30
Hawai-Oahu	0.0	1063	[75]
Hawaii-Mokapu	13.2	49	[75]
Hawaii-pooled	20.3	148	[75]
New Britain	0.0	85	[75]
New Ireland	0.0	53	[75]
Solomon Islands	0.0	50	[75]
New Caledonia	2.9	85	[75]
New Hebrides	0.0	84	[75]
Fiji	0.0	32	[75]
Society Islands	0.0	58	[75]
Lesser Sundas	0.0	45	[75]
Easter Island	8.6	64	[75]
Marquesas	2.8	51	[75]
Marquesas	18.2	36	[75]
Southern Cook Islands	3.8	52	[89]
Samoa	25	38	[89]
Island Melanesia	3.1	32	[89]
Duff Islands	6.1	59	[89]
New Guinea South Coast	3.3	95	[88]
New Guinea North/Melanesia	3.6	44	[88]
Canary Islands Galdár	64.7	34	[90]
Canary Islands Coast	40.2	97	[86]
Canary Islands fishing	8.6	105	[84]
Corondó, Brazil	0.0	32	[80]
Guaraguaçu, Brazil	13.3	30	[80]
Moro do Ouro, Brazil	18.9	37	[80]
Rio Comprido, Brazil	54.8	31	[80]
Base Aérea, Brazil	22.2	36	[80]
Tapera, Brazil	28.6	70	[80]
Cabeçuda, Brazil	43.2	74	[80]

<i>Site</i>	<i>Frequency (%)</i>	<i>n</i>	<i>Reference</i>
Middle Latitude (30° - 45°) “dry”			n = 19
Australia-Murray Valley	27.9	476	[75]
Australia-Murray Valley	21.2	99	[75]
Tasmania	4.8	62	[75]
Tasmania	9.0	67	[75]
Jomon, Japan	18.7	542	[89]
Yayoi, Japan	18.9	90	[89]
Çayönü, Turkey	17.5	97	[91]
Hopewell Mounds, IL	34.1	41	[75]
Klunk II, IL	34.0	78	[75]
Woodland, IL	2.0	50	[75]
Texas pooled	10.3	348	[92]
Pecos Pueblo, NM	2.4	500	[75]
Gran Quivira, NM	3.0	35	[75]
Grasshopper, AZ	0.0	161	[75]
Point of Pines, AZ	4.9	82	[75]
Turkey Creek, AZ	0.0	104	[75]
Pyramid Lake, NV	0.3	59	[75]
North Chile highland	0.0	549	[78]
North Chile valley	2.3	264	[78]
Middle Latitude (30° - 45°) “wet”			n = 15
Iron Gates pooled	29.4	126	[82]
Indian Knoll, KY	34.9	404	[76]
Isola Sacra	12.5	957	[81]
Isola Sacra	31.3	48	[93]
Velia	18.6	348	[81]
Muge pooled	19.4	72	[82]
Sado pooled	9.1	33	[82]
Vlasac Iron Gates	34.2	38	[79]
Santa Rosa Island early	8.1	62	[77]
Santa Rosa Island middle	13.9	72	[77]
Santa Rosa Island late	9.6	73	[77]
North Chile fertile coast	30.6	284	[78]
North Chile dry coast	30.8	52	[78]
Argentine wetlands	6.3	176	[94]
Körtik Tepe	48.1	81	[95]
High Latitude (>45°) “dry”			n = 18
North China	0.0	100	[75]
Ainu Hokkaido	1.6	128	[75]
Stuttgart-Mülhausen	5.0	60	[82]
Gurgy, France	2.1	48	[82]
Vaud-Valais	0.0	94	[82]
Southeast Scotland	0.0	50	[75]
York, UK	0.0	52	[75]
Hythe, UK	0.0	50	[75]
Salish interior	3.4	87	[75]
Inuit Yukon	2.0	50	[75]
Inuit St. Lawrence	2.0	50	[75]
Arikara/Mandan	21.1	109	[96]
Arikara-Crow Creek	2.3	613	[75]
Arikara-Mandan	8.8	34	[75]
Mandan	4.4	45	[75]

<i>Site</i>	<i>Frequency (%)</i>	<i>n</i>	<i>Reference</i>
Tierra-del-Fuego inland	1.9	53	[83]
Franzhausen	20.0	375	[97]
Mikulčice pooled	6.6	882	[98]
High Latitude (>45°) “wet”			n = 16
Hebrides	0.0	50	[75]
Shetlands	0.0	50	[75]
Iceland	0.0	82	[75]
Greenland	0.0	51	[75]
Inuit coastal	0.0	50	[75]
Pre-Aleut, AK	0.0	47	[75]
Aleut, AK	0.0	50	[75]
Salish coastal	6.5	107	[75]
Koskimo, BC	0.8	143	[75]
<i>Site</i>	<i>Frequency (%)</i>	<i>n</i>	<i>Reference</i>
Cowichan, BC	2.1	117	[75]
Haida, BC	0.0	36	[75]
Chinook, WA/OR	27.7	83	[75]
Tierra-del-Fuego coastal	9.1	55	[83]
Lower Volga Bronze Age	2.8	143	[99]
Na Pískách Old Slavonic	1.8	893	[100]
Vysoká zahrada Old Slavonic	1.5	129	[100]

External auditory exostoses among western Eurasian late Middle and Late Pleistocene humans

Supplementary Information

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S1 Later Pleistocene and Recent Human Auditory Exostoses

Table S3. Distributions of external auditory exostosis grades among the recent human samples providing grades of severity.

	<i>Grade 0</i>	<i>Grade 1</i>	<i>Grade 2</i>	<i>Grade 3</i>	<i>n</i>	<i>Ref</i>
Vaud/Valais (pooled) (“dry”) ^{1,2}	100%	--	--	--	83	[82]
Khoisan (“dry”)	100%	--	--	--	123	[88]
Gurgy (“dry”) ²	97.1%	2.9%	--	--	35	[82]
Stuttgart-Mülhausen (“dry”) ²	95.6%	4.4%	--	--	45	[82]
New Guinea coast (south) (“wet”)	96.7%	--	3.3%	--	92	[88]
Melanesian (north) (“wet”)	95.3%	4.7%	--	--	43	[88]
Santa Rosa Island (pooled) (“wet”)	89.8%	7.2%	2.4%	0.6%	166	[77]
Chile-Late Period (“wet”)	78.2%	11.9%	5.9%	4.0%	101	[77]
Muge (pooled) (“wet”) ²	76.0%	22.0%	2.0%	--	50	[82]
Iron Gates (pooled) (“wet”) ²	75.2%	20.8%	4.0%	--	101	[82]
Chile-Archaic Period (“wet”)	72.3%	22.3%	4.3%	1.1%	94	[78]
Isola Sacra (“wet”)	68.8%	20.8%	6.3%	4.2%	48	[93]
Chile-Formative (“wet”)	61.3%	21.3%	12.0%	5.3%	75	[78]
Körtik Tepe (“wet”)	51.9%	34.6%	4.9%	8.6%	81	[95]
“Dry” average	98.2%	1.8%	0.0%	0.0%		
“Wet” Average	76.6%	16.6%	4.5%	2.4%		

¹ See Table S2 for an explanation and a justification of “wet”/“dry” attributions.

² Data from the side with the largest sample.

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