

Morphological Adaptation to Climate in Modern *Homo sapiens* Crania: The Importance of Basicranial Breadth

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ABSTRACT

The aim of this study is to investigate whether the variation in breadth of the cranial base among modern human populations that inhabit different regions of the world is linked with climatic adaptation. This work provides an examination of two hypotheses. The first hypothesis is that the correlation between basicranial breadth and ambient temperature is stronger than the correlation between temperature and other neurocranial variables, such as maximum cranial breadth, maximum neurocranial length, and the endocranial volume. The second hypothesis is that the correlation between the breadth of the cranial base and the ambient temperature is significant even when other neurocranial features used in this study (including the size of the neurocranium) are constant. For the sake of this research, the necessary neurocranial variables for fourteen human populations living in diverse environments were obtained from Howells' data (except for endocranial volume which was obtained by means of estimation). The ambient temperature (more precisely, the mean yearly temperature) of the environments inhabited by these populations was used as a major climatic factor. Data were analysed using Pearson correlation coefficients, linear regression and partial correlation analyses. The results supported the two hypotheses, thus suggesting that ambient temperature may contribute to the observed differences in the breadth of the cranial base in the studied modern humans.

Key words: variation in basicranial breadth, adaptation to climate, modern humans

Introduction

Some of the first attempts to explain body morphology in terms of climatic adaptation were described by Bergmann¹ and Allen². Their observations were converted to the ecogeographic rules that were first applied to polytypic species of animals (mammals) and, more recently, have been commonly used to describe modern humans^{3–7}. The variation in human body size, as well as some features of the body shape like trunk and limb proportions, is currently recognised to be partially explicable as a climatic adaptation visible in external body morphology. The major differences in body form between humans inhabiting diverse geographic regions of the world are mainly explained by the thermoregulatory principle of increasing and decreasing body surface area/body mass in cold and hot climates (surface area/body mass is minimised in colder climates and maximised in

warmer climates)⁷. Variation in the external morphology of the head, particularly general head size and head shape^{8–13}, including nasal form and shape of the face^{14–20}, is thought to be another feature of human adaptation to climatic stresses.

In this paper, we focus only on neurocranial characteristics, such as maximum length and maximum breadth of the cranial vault (often referred to as cranial index) and brain size (estimated by endocranial volume), in relation to climate. Beals⁸ and Beals et al.^{10,11} indicated that the shape of the human head, cranial shape (cephalic and cranial indices) and head size (endocranial volume) are mainly related to the climatic variable of temperature. They suggested that larger, more rounded crania tend to be associated with colder climates and that

this observation is in accordance with Allen's and Bergmann's rules. Guglielmino-Matessi et al.⁹ computed the correlation between Howells' discriminant functions based on his cranial data²¹ and climatic data encompassing several measures of temperature and humidity. The results of their research indicated that the first discriminant function had its highest values among modern human populations that live in the coldest climates and its lowest value among populations living in the warmest climates. Among cranial measurements, the breadth of the cranial base (biauricular breadth) and the maximum breadth of the neurocranium contributed the most to this discriminant function. Guglielmino-Matessi et al.⁹ recognised that the first discriminant function was significantly correlated with general cranium size and failed to notice the relationship between the basicranial breadth and the cranial adaptation to climate. They stressed the importance of the high correlation between low temperature and cranial vault breadth and concluded that the results of their study are in agreement with the suggestion of Coon et al.²² that human crania in colder climates tend to be larger and broader. Their conclusions were consistent with the results of Beals et al.¹¹, which showed that, among three measurements of modern human crania (maximum cranial breadth, maximum cranial length and height), the greatest contribution to the endocranial volume derives from the first of these features, followed by the length and height of the neurocranium. Many authors have accepted the opinion that the evolutionary morphological response to climate in human neurocrania is reflected in the variation found in the shape of the cranial vault (value of cranial index) and the variation in the endocranial volume^{7,10–13,19}. However, the relationship between climate and the variation in breadth of the basicranium has not been noticed.

The cranial base is the region of the vertebrate skull that is widely regarded as the most ancient and vestigial structure and shows high conservation across phylogeny^{13,19,23–27}. Studies of the pattern of covariation within and among functional and developmental regions of the skull (the cranial modules) in mammals^{28,29} and primates³⁰ have indicated that the basicranial region is one of the most highly integrated structures of the cranium. In modern humans, cranial base breadth influences the overall shape of the cranium, constraining cranial vault breadth and facial breadth. Recently, it has been shown that the genetic correlation between the breadth measures of the cranial base, cranial vault and the face are high, and play a key role in the patterns of integration of the human skull²⁷. Martínez-Abadías et al.²⁷ have provided empirical evidence that covariation between the width of the cranial regions mentioned above is one of the dominant factors of integration in the human skull. They extended this pattern of skull integration, which was first reported in the mouse cranium³², to humans and suggested that this pattern indicated a high level of conservation across the evolution of the mammalian skull form. The results of their research stressed the great importance of basicranial width in the integrated

development of the human skull and supported previous findings implicating the cranial base as the skull's »key integrator«^{31,33,34}. Taking into account the great importance of the basicranial breadth in skull integration and its influence on the shape of the cranial vault, we assume that variation in modern human neurocrania linked with climatic adaptation can be mainly related to variation in the breadth of the cranial base. Our assumption also suggests that cranial base breadth likely has a stronger relationship with climate than do other neurocranial features examined here.

Thus, the aim of our study is to test two hypotheses. The first hypothesis is that basicranial breadth is more highly correlated with ambient temperature than the other neurocranial variables analysed here (maximum cranial breadth, maximum neurocranial length, and endocranial volume) in modern human populations. The second hypothesis is that the correlation between basicranial breadth and ambient temperature is significant even if each of the remaining neurocranial variables studied is kept constant. We used Howells' data³⁵ concerning neurocranial measurements (including biauricular breadth as the basicranial breadth measure) for fourteen modern human populations from different geographic regions of the world. The endocranial volume for each human skull was estimated based on multiple regression analyses described by Beals et al.¹¹ Three types of temperature information are used for each geographic region inhabited by the examined human populations, and we predict that the correlation should be highest between the neurocranial variables and the lowest temperature. This prediction is based on the results of many studies suggesting that cold stress is a major climatic factor that influences human neurocranium morphology^{9,11}.

The *Homo sapiens* crania sample examined here includes crania from the Siberian (Buriat) population, which is an example of a human group living in extreme climatic conditions and exhibiting a very broad cranial base and vault. Recently, Roseman¹² and Harvati and Weaver¹³ has stressed the problematic impact the Siberian population has had on the model of the relationship between climatic variables and cranial morphology upon its inclusion in the examined sample of modern humans. Taking into account the suggestion mentioned above, we also predict that the correlation between basicranial breadth and temperature (three types of this main climatic indicator are used here) should be highest relative to the correlation between other neurocranial variables and ambient temperature in sample of modern human crania, even excluding the Buriat population. In order to describe the general relationship between ambient temperature and the neurocranial features examined here, we use the mean yearly temperature instead of the other two measures of this climatic factor used in this study: mean temperature in the coldest month and mean temperature in the hottest month. We regard the mean yearly temperature as the most appropriate temperature to test our main hypotheses (all three temperature types were used only in the preliminary part of our analysis).

Materials

We have used data from the samples of adult modern human crania (males and females) examined by Howells^{21,35} for this study. The samples come from geographically diverse regions of the world (Europe, Africa, Asia, Australia and Greenland) (Table 1). Populations from North and South America were not included due to problems associated with the uncertain migration periods in this region⁷. For the same reason, Howells^{21,35}. Egyptian sample was excluded (we recognise that the possibility of human migrations from Near East or Europe to this region is very high). A group of crania from Peru was also excluded due to uncertain identification of the sites at which the skulls were excavated. The above-mentioned samples were excluded from this research in order to avoid problems concerning false interpretation of the relationship between the examined neurocranial variables of these human populations and the temperature of their geographic regions, a problem that was stressed by Beals⁸, who illustrated it with the Apaches. Human populations that inhabited small and medium-sized islands were also not included. According to Houghton³⁶ and Ruff⁷, the traditional way of life of these people often involved travelling in open boats over cool waters, so the climatic conditions of their living were likely modified by the influence of the temperature of the oceanic water. Ultimately, only fourteen cranial samples from those examined by Howells^{21,35} were chosen (Table 1).

Five neurocranial measurements were used to investigate our hypotheses: maximum cranial breadth (XCB), maximum neurocranial length (GOL), biauricular breadth (AUB), neurocranial height (BBH), and basion-nasion length (BNL). Information about these features was obtained from Howells³⁵ globally distributed craniometric data set. A detailed description of these measurements is shown in Table 2; summary statistics are

provided in Table 3. For each human population, three types of temperature information were collected: mean yearly temperature (MNT), mean temperature in the coldest month (CMT), and mean temperature in the hottest month (HMT) (Table 4). Temperature data were obtained from a German Karlsruhe weather service (Kima-daten; website: <http://www.wetterzentrale.de>) encompassing observations from many meteorological stations around the world. These data are accessible on website – <http://www.klimadiagramme.de/Frame/indexeu.html> and were collected from the meteorological stations nearest to the sites where the cranial samples were excavated. Records had been collected for 29 years, from 1961 to 1990 (Tables 1 and 4). Here, we focus only on temperature because this climatic variable was used most frequently and appeared to have a greater impact on cranial morphology than the remaining climatic factors (e.g., total, minimum and maximum yearly precipitation; measures of humidity) used in other studies of climate influence on the morphology of the human body^{8–11,15,17–19,36,37}. In spite of the fact that for some cranial samples we applied known temperature information from the same meteorological stations as other authors, our data is not directly comparable with that obtained by other researchers due to the use of different climate datasets^{9,12,13}.

Methods

All measurements were analysed using Statistica version 8.0 (StatSoft, Inc.2008). It is worth noting that Howell's data used in this study do not contain information about the endocranial volume of the examined skulls; thus, we used the multiple regression calculated by Beals et al.¹¹ between the endocranial volume and three external cranial measurements (XCB, GOL and BBH) in order to assess this feature for each analysed

TABLE 1
MATCHED POPULATIONS IN HOWELL'S SERIES OF CRANIOMETRIC DATA (WITH SAMPLE SIZES) AND SOURCE OF CLIMATIC VARIABLES

| Populations n – 1314 | n | Stations for climate variables |
|--|-----|--|
| Oslo (Norse) | 110 | Gardermoen, Oslo |
| Zalavár (Hungary) | 98 | Budapest, Pecs, Szombathely |
| Berg (Carinthia, Austria) | 109 | Graz, Klagenfurt |
| Teita (Kenya) | 83 | Garissa, Nairobi |
| Dogon (Mali) | 99 | Bamako, Gao, Mopti, Segou |
| Bushmen (South Africa) | 90 | Pietersburg, Pretoria |
| Zulu (South Africa) | 101 | Bloemfontain, Kimberley, Upington, |
| Buriat (Siberia, Baikal region) | 109 | Irkutsk, Tschita, Ulan-Ude, Zigalovo |
| Ainu (South Central Hokkaido) | 86 | Asahikawa, Obihiro, Rumoi |
| Anyang (Shang Dynasty Chinese) | 42 | Peking, Taiyuan, Zhengzhou |
| North Japan | 87 | Kutchan, Sapporo, Sutsu |
| South Japan | 91 | Fukuoka, Kumamoto, Nagasaki |
| Inugsuk Eskimo (Greenland) | 108 | Angmagssalik, Frederikshab, Jakobshavn, Prins Chr.Sund |
| Lake Alexandrina Tribes (S. Australia) | 101 | Adelaide, Melbourne, Woomera |

TABLE 2
CRANIAL VARIABLES USED IN THIS STUDY

| ABBR. | Definition |
|-------|---|
| XCB | Maximum cranial breadth – perpendicular to sagittal plane; chord distance from left eurion to right eurion |
| GOL | Maximum neurocranial length – chord distance from glabella to opisthocranium |
| AUB | Biauriculare breadth (cranial basal breadth) – chord distance from left radiculare to right radiculare |
| BBH# | Neurocranial height – chord distance from basion to bregma |
| BNL# | Basion – nasion length (the anterior external length of the basicranium) – chord distance from basion to nasion |
| ECV | Estimated endocranial volume |
| GGM | Size of the neurocranium – geometric mean of six diverse cranial variables: XCB, GOL, AUB, BBH, BNL and ECV* |

– these measurements were used only to computation of the geometric mean

* the cube-root of estimated endocranial volume

specimen ($ECV_{cm^3} = -403.9 + (80.6 \times XCB) + (42.8 \times GOL) - (9.3 \times BBH)$). This multiple regression can be applied to sex-combined contemporary ethnic groups¹¹. We used the cube-root of the estimated endocranial volume (ECV) to

compare linear and volumetric data. In order to assess the size of the neurocranium for each skull, the geometric mean (GGM) of six cranial dimensions was computed as the sixth root of the product of the following variables:

TABLE 3
DESCRIPTIVE STATISTICS OF CRANIAL SAMPLES

| Populations | XCB | GOL | AUB | BBH | BNL | ECV | GGM |
|--|------------------|------------------|------------------|------------------|------------------|--------------------|------------------|
| Oslo (Norse) | 139.08 (5.30) | 184.23 (6.53) | 121.16 (5.24) | 128.84 (5.45) | 99.55 (4.20) | 1385.76 (60.49) | 128.16 (3.66) |
| Zalavár (Hungary) | 139.33 (4.77) | 181.14 (7.28) | 121.39 (4.80) | 132.05 (5.94) | 99.09 (4.77) | 1371.56 (58.36) | 128.22 (3.66) |
| Berg (Carinthia, Austria) | 144.08 (6.25) | 175.56 (8.49) | 124.02 (6.13) | 127.44 (5.37) | 95.83 (5.05) | 1390.28 (71.29) | 127.34 (4.14) |
| Teita (Kenya) | 127.79 (4.60) | 178.41 (6.82) | 114.41 (4.28) | 126.69 (4.78) | 98.72 (4.46) | 1271.90 (56.59) | 123.38 (3.37) |
| Dogon (Mali) | 134.65 (5.19) | 173.56 (6.97) | 112.22 (4.66) | 130.01 (4.95) | 96.58 (4.04) | 1303.30 (59.90) | 123.74 (3.46) |
| Bushmen (South Africa) | 130.85 (5.07) | 174.74 (6.77) | 110.15 (5.51) | 120.88 (5.09) | 93.07 (4.51) | 1286.27 (57.90) | 120.59 (3.67) |
| Zulu (South Africa) | 133.02 (5.19) | 182.32 (6.29) | 114.68 (6.14) | 131.42 (3.70) | 99.85 (1.54) | 1326.33 (56.12) | 125.99 (3.61) |
| Buriat (Siberia, Baikal region) | 151.66 (6.77) | 176.78 (7.66) | 132.78 (6.30) | 129.88 (5.68) | 99.30 (4.61) | 1454.31 (74.79) | 131.58 (4.21) |
| Ainu (South Central Hokkaido) | 140.00 (4.92) | 186.00 (7.62) | 122.50 (5.51) | 137.00 (5.17) | 104.00 (5.34) | 1392.99 (63.44) | 131.43 (4.20) |
| Anyang (Shang Dynasty Chinese) | 138.78 (5.42) | 181.00 (4.27) | 125.69 (4.85) | 140.26 (5.33) | 101.28 (4.07) | 1358.95 (46.66) | 130.58 (2.64) |
| North Japan | 138.62 (5.90) | 178.68 (8.54) | 121.59 (5.74) | 134.15 (6.82) | 99.33 (5.17) | 1353.36 (70.37) | 128.14 (4.51) |
| South Japan | 136.23 (4.90) | 177.33 (7.10) | 120.35 (5.01) | 134.97 (5.59) | 99.10 (4.76) | 1327.57 (53.89) | 127.35 (3.79) |
| Inugsuk Eskimo (Greenland) | 132.48 (4.73) | 184.55 (6.48) | 123.39 (4.89) | 135.90 (5.68) | 103.31 (4.72) | 1327.41 (50.41) | 129.17 (3.50) |
| Lake Alexandrina Tribes (S. Australia) | 129.79 (5.36) | 185.84 (7.47) | 116.79 (5.51) | 126.66 (5.87) | 99.16 (4.37) | 1319.83 (63.95) | 125.32 (4.08) |

See Table 2 for variables details and abbreviations

Linear measurements in mm, ECV in cm³, standard deviations in parentheses

TABLE 4
CLIMATIC VARIABLES USED FOR EACH CRANIAL SAMPLE

| Cranial sample | MNT | CMT | HMT |
|-------------------------|-------|--------|-------|
| Oslo | 4.75 | -5.75 | 15.80 |
| Zalavár | 10.00 | -1.63 | 20.46 |
| Berg | 8.05 | -3.95 | 18.55 |
| Teita | 23.85 | 21.90 | 25.60 |
| Dogon | 28.47 | 23.62 | 33.22 |
| Bushmen | 17.85 | 11.50 | 22.20 |
| Zulu | 18.06 | 9.73 | 25.23 |
| Buriat | -1.92 | -24.20 | 17.82 |
| Ainu | 6.66 | -7.23 | 20.46 |
| Anyang | 11.90 | -3.36 | 25.53 |
| North Japan | 7.63 | -4.53 | 21.00 |
| South Japan | 16.40 | 5.70 | 27.60 |
| Inugsuk Eskimo | -1.57 | -8.50 | 6.60 |
| Lake Alexandrina Tribes | 16.70 | 10.60 | 22.90 |

Temperatures are reported in degrees Celsius (MNT – mean yearly temperature, CMT – mean temperature in the coldest month, HMT – mean temperature in the hottest month)

XCB, GOL, AUB, BBH, BNL and the cube-root of the estimated endocranial volume (ECV) (Tables 2 and 3). We examined the relationship between neurocranial variables (XCB, GOL, AUB, cube-root of ECV and GGM) and three types of data concerning temperature: MNT, CMT and HMT. Our examination was performed twice, first in the total sample of modern human populations used here and second after excluding the Buriat population, with the use of Pearson correlation coefficients. Additionally, the traits: AUB, XCB and GOL were divided by GGM in order to eliminate the size differences of the skulls. To assess the strength of the relationship between variables obtained in this way and MNT, the Pearson correlation coefficients were applied (this analysis was carried out twice; first for the entire sample of studied crania and then after excluding Buriat’s skulls). Moreover, to establish if the Pearson correlation coefficient between AUB/GGM and MNT is in fact significantly higher when compared to the Pearson correlation coefficients of each remaining variable (XCB/GGM, GOL/GGM, XCB/ GOL) and MNT, test Z for comparison of the values of these types of coefficients was applied – This test was also carried out on the entire sample of crania and then again after removing Buriat’s skulls. The partial correlations between mean yearly temperature and the neurocranial features were used in order to keep each neurocranial variable constant (in two samples of modern human populations mentioned above). This temperature variable illustrates the general relationship between ambient temperature and the examined features of the human neurocranium. Linear regression analyses were also used to estimate the proportion of variance of each neurocranial variable used in this study by MNT (in the total sample of human populations).

Results

Correlation analysis (Table 5) indicates that biauricular breadth is more significantly and highly correlated with each of the three temperature measures used in this study than any of the other analysed neurocranial variables. This correlation was observed not only in the sample including all examined populations but also in the sample without the Buriat population. This observation supports our first hypothesis. It is worth stressing that the correlation between basicranial breadth and mean temperature in the coldest month is higher than the correlation between the same neurocranial feature and other measures of temperature in both types of modern human cranial samples mentioned above. The same regularity is also observed in the case of the maximum cranial breadth and the endocranial volume (with one exception of maximum neurocranial length) (Table 5). This regularity supports the first prediction, which suggests that »cold stress« has a greater influence on cranial morphology than »hot stress«. The results also indicate that the correlation between each neurocranial variable (except GOL) and all measures of temperature becomes somewhat lower when the Buriat population is removed from the modern human sample than when all examined populations are included. Nevertheless, this correlation is still high and significant. This result confirms the second prediction, which is that the exclusion of the Siberian population from the examined modern human sample should not result in the disappearance of the relationship between the analysed neurocranial variables and ambient temperature.

All correlations in analysed neurocranial variables against the MNT are significant (see Table 5). The correlation between cranial index (XCB/GOL) and this measure of temperature is moderate ($r=-0.30$, $p<0.01$) and higher only in comparison to the correlation between GOL and the same type of temperature (Table 5 and Figures 1–5). According to the linear regression analyses, MNT accounts for approximately 40% of the variation in

TABLE 5
CORRELATIONS BETWEEN NEUROCRANIAL VARIABLES AND THE THREE TEMPERATURE MEASUREMENTS IN SAMPLE INCLUDING ALL HUMAN POPULATIONS USED IN THIS STUDY AND SAMPLE THAT EXCLUDE THE BURIAT POPULATION

| Variable | r (total sample) | | | r (sample without Buriat) | | |
|----------|------------------|-------|-------|---------------------------|-------|-------|
| | MNT | CMT | HMT | MNT | CMT | HMT |
| XCB | -0.47 | -0.60 | -0.17 | -0.32 | -0.44 | -0.11 |
| GOL | -0.18 | -0.11 | -0.23 | -0.27 | -0.24 | -0.27 |
| AUB | -0.63 | -0.69 | -0.41 | -0.54 | -0.59 | -0.39 |
| ECV* | -0.47 | -0.55 | -0.25 | -0.36 | -0.44 | -0.21 |

See Table 2 for variables details and abbreviations
All correlations are significant ($p<0.01$), MNT – mean yearly temperature, CMT – mean temperature in the coldest month, HMT – mean temperature in the hottest month (Celsius degrees), * – the cube root of estimated endocranial volume

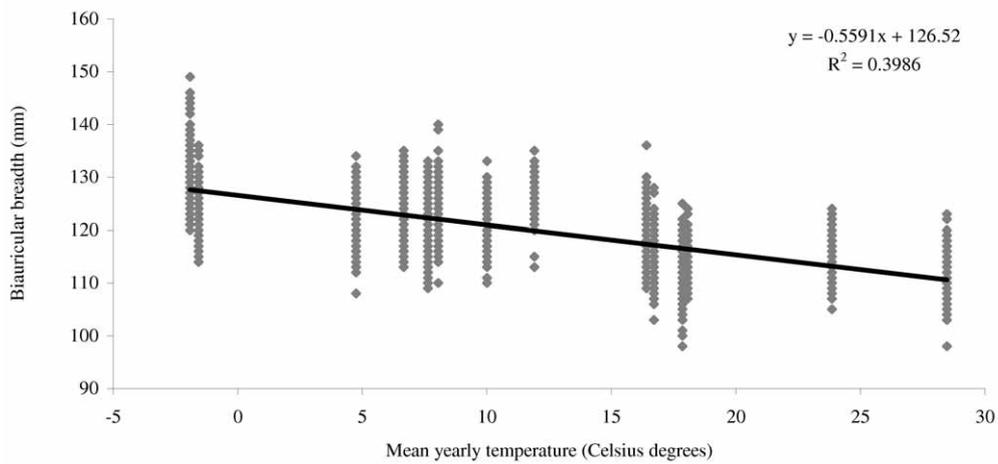


Fig. 1. Change in biauricular breadth (AUB) with mean yearly temperature in human populations (data from Table 4).

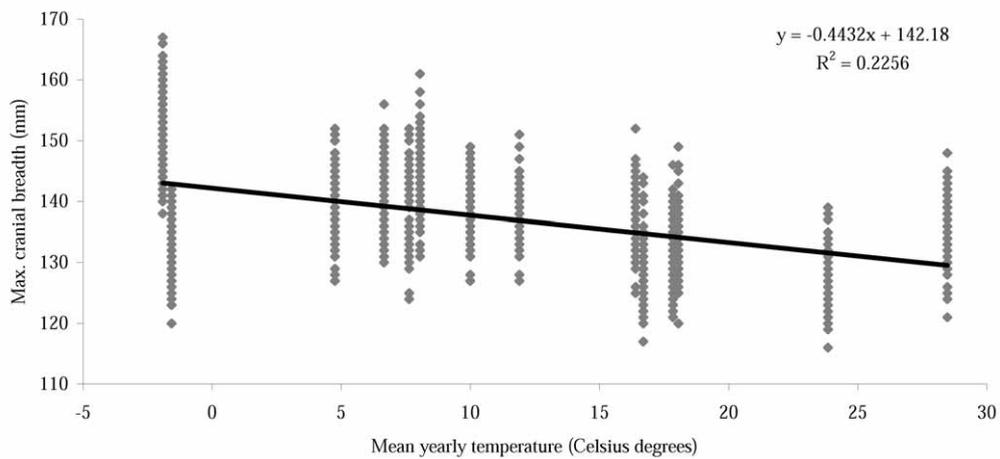


Fig. 2. Change in max. cranial breadth (XCB) with mean yearly temperature in human populations (data from Table 4).

AUB, 20% of the variation in each of the next two features (XCB and ECV), 3% of variation in GOL, and 9% of variation in XCB/GOL in the modern human sample

studied here, including the Buriat population (Figures 1–5). It is important to stress that the correlation between AUB and MNT is high ($r = -0.63$, $p < 0.01$) (Tables 5

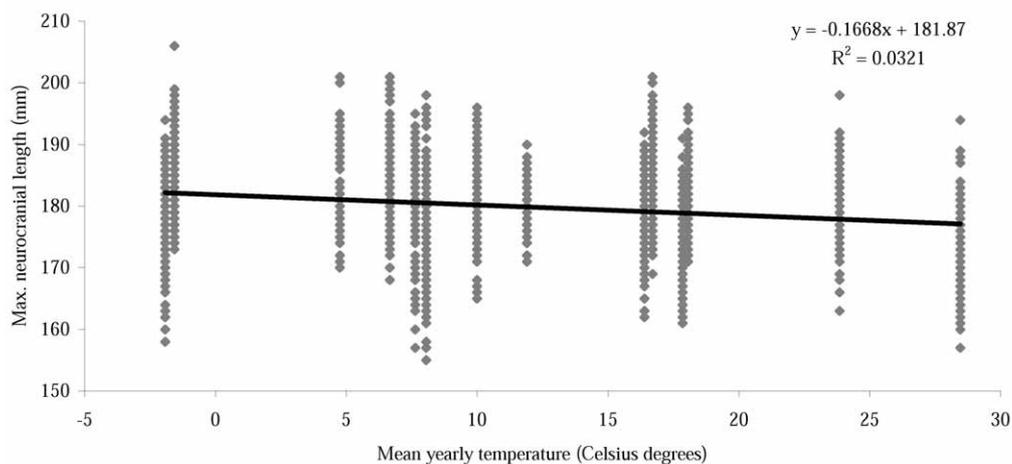


Fig. 3. Change in max. neurocranial length (GOL) with mean yearly temperature in human populations (data from Table 4).

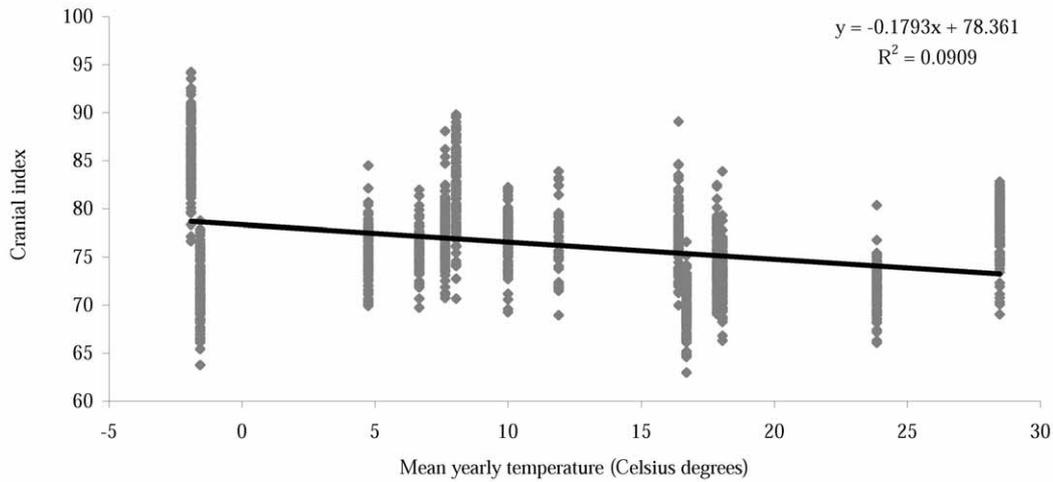


Fig. 4. Change in cranial index (XCB/GOL) with mean yearly temperature in human populations (data from Table 4).

and 6) and that the percentage of the variation in AUB that is explained by the influence of MNT on this cranial feature is higher than the percentage that explains the influence the same temperature measure has on the other studied neurocranial variables (Figures 1–5). This result confirms that basicranial breadth can play a key role in cranial morphological adaptation to climate and, thus, supports the second hypothesis.

In the case of an additional analysis concerning variables: AUB/GGM, XCB/GGM, GOL/GGM and also XCB/GOL the results indicate that for the entire sample of crania the Pearson correlation coefficients between the examined variables and MNT are significant (the correlation coefficients of each individual variable and MNT account for: AUB/GGM $r_1 = -0.59$, $p < 0.01$; XCB/GGM $r_2 = -0.24$, $p < 0.01$; GOL/GGM $r_3 = 0.30$, $p < 0.01$; XCB/GOL $r_4 = -0.30$, $p < 0.01$). The results of the test comparing the two Pearson correlation coefficients indicate that the correlation coefficient between AUB/GGM and MNT

(r_1) is significantly different from the correlation coefficients of the other variables (mentioned above: from r_2 to r_4) and MNT: (r_1 in comparison with; $r_2 - U = -11.12$, $p < 0.01$; $r_3 - U = -25.28$, $p < 0.01$; $r_4 - U = -9.38$, $p < 0.01$). The results of the analogous calculations conducted on the sample of crania that excluded the Buriat's skulls, show that the correlation coefficients of the examined variables with MNT are significant: (AUB/GGM $r_1 = -0.47$, $p < 0.01$; GOL/GGM $r_3 = 0.12$, $p < 0.01$; XCB/GOL $r_4 = -0.30$, $p < 0.01$) excluding XCB/GGM ($r_2 = -0.01$, $p > 0.01$). The Pearson correlation coefficient between AUB/GGM and MNT (r_1) is significantly different in comparison to the correlation coefficients of the other variables (mentioned above) and MNT (r_1 in comparison with; $r_2 - U = -12.23$, $p < 0.01$; $r_3 - U = -15.48$, $p < 0.01$; $r_4 - U = -5.06$, $p < 0.01$). The results obtained indicate the presence of a significant correlation between AUB/GGM and MNT, which is significantly stronger than the correlations between other variables (GOL/GGM, XCB/GGM,

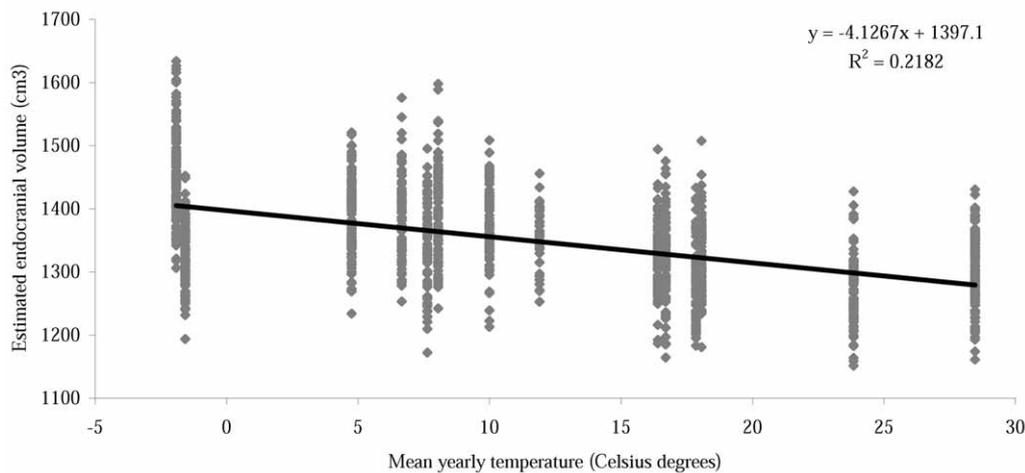


Fig. 5. Change in endocranial volume (ECV) with mean yearly temperature in human populations (data from Table 4).

TABLE 6
CORRELATIONS BETWEEN NEUROCRANIAL VARIABLES AND MEAN YEARLY TEMPERATURE IN SAMPLE INCLUDING ALL HUMAN POPULATIONS USED IN THIS STUDY

| Partial r | | | | | | |
|-----------|-------|--------------|--------------|--------------|---------------|--------------|
| Variable | r | XCB constant | GOL constant | AUB constant | ECV* constant | GGM constant |
| XCB | -0.47 | — | -0.46 | (0.03) | -0.14 | -0.21 |
| GOL | -0.18 | -0.11 | — | 0.08 | 0.12 | 0.25 |
| AUB | -0.63 | -0.47 | -0.62 | — | -0.48 | -0.47 |
| ECV* | -0.47 | -0.10 | -0.45 | 0.06 | — | -0.11 |
| GGM | -0.49 | -0.24 | -0.51 | 0.12 | -0.19 | — |

See Table 2 for variables details and abbreviations

Correlations in parentheses are nonsignificant ($p > 0.01$), * the cube-root of estimated endocranial volume

TABLE 7
CORRELATIONS BETWEEN NEUROCRANIAL VARIABLES USED IN THIS STUDY AND MEAN YEARLY TEMPERATURE IN SAMPLE EXCLUDING BURIAT POPULATION

| Partial r | | | | | | |
|-----------|-------|--------------|--------------|--------------|---------------|--------------|
| Variable | r | XCB constant | GOL constant | AUB constant | ECV* constant | GGM constant |
| XCB | -0.32 | — | -0.26 | 0.09 | (0.02) | (-0.03) |
| GOL | -0.27 | -0.20 | — | (-0.01) | (-0.04) | 0.09 |
| AUB | -0.54 | -0.47 | -0.49 | — | -0.44 | -0.37 |
| ECV* | -0.36 | -0.19 | -0.25 | (0.07) | — | (0.01) |
| GGM | -0.44 | -0.32 | -0.36 | (0.06) | -0.26 | — |

See Table 2 for variables details and abbreviations

Correlations in parentheses are nonsignificant ($p > 0.01$), * the cube-root of estimated endocranial volume

XCB/GOL) and MNT (it is worth noting that this regularity is observed, even when the Buriat's skulls are excluded from the examined sample).

The correlation between MNT and each of the neurocranial variables as well as partial correlations between MNT and these variables with each feature kept constant are listed in Tables 6 and 7 (the first table includes data for the sample of modern humans including the Buriat population, while the second table includes data for the sample without the Siberian population). In the case of the total sample of modern human populations studied here, the results indicate that the correlation of the AUB with MNT is high, while the partial correlation of AUB on MNT when XCB is kept constant decreases to a moderate level ($r = -0.47$, $p < 0.01$) (Table 6). When variation in AUB is controlled, the correlation between XCB and MNT vanishes completely ($r = 0.03$, $p > 0.01$). The partial correlation between AUB and MNT with ECV kept constant also decreases to a moderate level ($r = -0.48$, $p < 0.01$); however, the partial correlation of ECV on MNT decreases significantly if AUB is held constant ($r = 0.06$, $p < 0.01$) (Table 6). These results suggest that the correlation between XCB and MNT, and also between ECV and MNT, is due largely to variation in AUB related to adaptation to climate. The partial correlation between AUB and MNT when GOL is kept constant ($r = -0.62$, $p < 0.01$) is nearly the same as the corre-

lation between AUB and MNT ($r = -0.63$, $p < 0.01$); when AUB is controlled, the correlation between GOL and MNT decreases significantly ($r = 0.08$, $p < 0.01$) (Table 6). This result, and the observation that GOL is least correlated with MNT among the neurocranial variables studied, suggests that the relationship between AUB and GOL is weaker than the other neurocranial features studied here. The results also show that the correlation between XCB and MNT is moderate ($r = -0.47$, $p < 0.01$) and that the partial correlation of XCB and MNT decreases significantly when ECV is kept constant ($r = -0.14$, $p < 0.01$) (Table 6). This change suggests that there is a relationship between XCB and ECV, consistent with the results of other research (e.g.,^{11,31}). Furthermore, the GGM was used to examine how this variable influences the relationship between AUB and MNT. When the variation in GGM is controlled, the partial correlation between AUB and MNT decreases to a moderate level ($r = -0.47$, $p < 0.01$). However, if AUB is controlled, the partial correlation between GGM and MNT decreases and becomes weak ($r = 0.12$, $p < 0.01$) in comparison to the correlation of GGM with MNT ($r = -0.49$, $p < 0.01$) (Table 6). This result suggests that, as in the case of XCB and ECV, the correlation between GGM and MNT depends significantly on the variation in AUB. The results described above support our assumption that the basi-cranial breadth plays one of the major roles in the mor-

phological adaptation of the modern human neurocranium to ambient temperature.

When excluding the Siberian population from the modern human sample, the partial correlation analyses between MNT and neurocranial variables, while keeping other features constant, have a pattern of changes similar to that observed in the total sample (this pattern of changes concerns the partial correlation between AUB and MNT when the other neurocranial variables are constant and also the partial correlation between neurocranial variables: XCB, ECV, GGM and MNT when the variation in AUB is controlled) (Table 7). It is important to note that the partial correlation of GOL (as well as ECV and GGM) with MNT disappears if variation in AUB is controlled (Table 7). The results concerning this sample also support our opinion that the adaptation of modern human cranial morphology to climate is probably connected to a great extent with variation in basicranial breadth.

Discussion and Conclusion

The results of our study clearly indicate that the breadth of the cranial base is more highly correlated with ambient temperature than other neurocranial variables analysed here in the modern human sample. We also show that this relationship is present even when each of the other neurocranial variables is kept constant. These observations support our assertion that the breadth of the cranial base may play a key role in cranial morphological adaptation to climate. The main conclusion of our research is that the geographic distribution of basicranial breadth in modern human populations can be interpreted in terms of adaptation to different climatic conditions. A relationship between the breadth of the cranial base and the climate has not been shown previously. Our observations – that modern human cranial morphology in colder climates tends towards a broader cranial vault and a larger neurocranium (as well as larger endocranial volume) and that the correlation between ambient temperature and endocranial volume is higher than in the case of cranial index (XCB/GOL) (see Figures 1–5) – are in agreement with the studies of Guglielmino-Matessi et al.⁹ and Beals et al.¹¹. In the sample of modern human crania used in our study, the relationship between the ratio of basicranial breadth to cranial size and mean yearly temperature (when excluding the Buriat population) is significant and significantly higher than the correlation of the ratios of other neurocranial features to size (and Cranial index) with this temperature data. This result indicates that there is a general trend in the variation of basicranial breadth in modern human populations (lower ambient temperature is correlated with broader cranium base), which results from differences in climatic conditions. Nevertheless, this study has some limitations. First, we used estimated endocranial volume for each of the examined crania. This procedure inevitably produces some discrepancy between estimated and actual endocranial volume. Thus, we should be careful with the in-

terpretation of our results concerning ECV (and also GGM) as these variables were calculated from other traits. Unfortunately, it was not possible to collect the real ECV of each skull included in this study. Second, we realise that the information used here concerning ambient temperature cannot correspond exactly to the real climatic conditions experienced by individuals in the examined human populations. This issue was also stressed by Guglielmino-Matessi et al.⁹ but unfortunately, no better solution to this problem has been found. Thus, the data related to the ambient temperature obtained from meteorological stations are still used by many authors in their studies^{12,13,19}, including ours.

Hernández et al.¹⁸ have shown that the crania of human tribes that inhabited Tierra del Fuego – a region below 55°S, characterised by a very cold climate – showed unusually high values for biauricular breadth in comparison to other human populations that they had examined. This observation is in accordance with our results, which suggest a significant relationship between ambient temperature and this cranial feature (lower ambient temperature is correlated with a broader base of the cranium). The results of our study are also consistent with Roseman's¹² observation that the crania of human populations living in cold environments show large neurocranial breadth measurements. Recently, Harvati and Weaver¹⁹ and Smith et al.³⁸ have concluded that the centroid size of the human temporal bone is significantly correlated with ambient temperature in modern humans. This observation is also consistent with our results, as AUB is the distance between two points located on the temporal bones measuring some of the same dimensions as temporal bone centroid size. Nevertheless if the estimated cranial size (GGM) is kept constant, then the partial correlation between basicranial breadth is still significant; hence, the relationship between AUB and ambient temperature does not result only from the change in the size of the cranium. In our opinion, it is highly probable that measures basicranial breadth other than AUB will also show a significant correlation with the ambient temperature, although this assumption should be examined.

Bastir et al.³⁹, Bastir and Rosas^{40,41} recently highlighted that the midline and lateral basicranial structures exhibit different growth patterns in modern humans (the shape of the midline cranial base is established earlier in ontogeny than the lateral basicranium, which matures later, in puberty). The physical contact between mandible and the base of the cranium occurs at the lateral parts of this structure (in the glenoid fossa) to a significant degree⁴¹. Moreover, the results of many studies support a relationship between mandibular variation and the morphology of the lateral parts of the cranial base^{40,42}. Our observation that humans inhabiting cold regions show wider basicranial breadth than humans living in hot regions is in agreement with studies on variation in the morphology of modern human mandibles. Such studies suggest that the medio-lateral breadth of the mandible reflects climatic adaptation (temperate and cold-climate human groups show wide medio-lateral man-

dibles)²⁰. The mandibles of arctic human populations show an extremely wide bicondylar breadth⁴³. Nicholson and Harvati²⁰ stressed that the occurrence of this feature in these cold-climate populations cannot be explained as a response to biomechanical stress, as suggested earlier by Hylander⁴³. Taking into account the integration between mandible and base of the cranium mentioned above, we suggest that the pattern of variation in bicondylar breadth should be consistent with the climatic patterning of basicranial breadth.

Some authors^{12,18} don't regard this hypothesis — that the shape of the human cranial vault is under influence of climatic conditions — as a general rule. They have stressed, for example, that some Eskimo groups living in very harsh environments are dolichocephalic and that dolichocephaly was the common feature of Pleistocene hominins living in cold climates¹⁸. From our point of view, this problem concerns the method of verifying hypotheses about the relationship between cranial morphology and climate. In order to make such a verification, we should know from which region of the world (i.e., from which population) the studied sample of modern humans comes. We should also take in to account information about the climatic conditions of the region inhabited »earlier« by the »parental« population as well as the region inhabited after migration, at the site where the skulls were excavated. The direction of cranial shape change (not the shape of the cranium, which is usually described by cranial index) as well as its accordance with the direction of climatic changes should be examined. Hence, we must take into account information about population history (particularly migrations) and the origin of the studied populations for the sake of a correct assessment. We realise that there are many limitations in this method. First, we do not know how much time is needed for changes in cranial shape to evolve after colonisation of a new region with new climatic conditions; second, we assess the direction of change in some features (e.g., breadth of the neurocranium, breadth of basicranium), which can be also influenced by other cranial features that are connected with the highly integrated structure of the human skull^{27,41} and environmental factors other than ambient temperature (e.g., response to biomechanical stress^{18,44}). Then, we usually have limited information about the origin and history of the examined human populations. These problems are much more visible in the case of fossilised human beings because our knowledge about climate change during these periods (e.g., in the Pleistocene) and about the migrations of the hominins is not deep enough to approximate the real climatic conditions of the geographic regions they inhabited and their real migration paths.

Climatic conditions are usually assumed to affect the size and shape of the human body, including the head, as a reflection of thermoregulatory mechanisms (Bergmann's rule)^{10,12,38}, however, the »process« of cranial morphological adaptation to climate is not well understood^{13,18,38,45}. Rae et al.⁴⁵ have shown that significant changes can be observed in rat cranial morphology as a developmental

response to cold stress. Taking this observation into account, we cannot exclude the possibility that the developmental response to ambient temperature (developmental plasticity) is also significant for the adaptation of human cranial morphology to climate. Future investigations should address the above-mentioned problem.

It should be stressed that diet, means of subsistence and physical activity all impact on human neurocranial shape and size. Diet related factors such as protein deficiencies and the softer consistency of the food consumed after the transition to food production, are linked to a reduced cranial size and therefore, to a reduction in both the breadth and length of the cranial vault in human populations^{46,47}. The reduced mobility of sedentist living is interpreted as an influential factor in the reduction of growth hormone circulation, which leads to a smaller sized crania as in the case of the farmers when compared to that of the hunter-gatherers' crania⁴⁶. With the cranial data used in our study, we were not able to explicitly incorporate how »manipulating« these developmental environmental factors would impact on neurocranial morphology. There is too little information available regarding the type of diet and means of subsistence of the individuals in our samples, although we can be certain that most of the individuals included in our study came from populations practicing some type of agriculture^{21,35}. Further studies are needed to establish the extent to which the developmental environmental factors influence cranial vault shape and size. The intra-group analyses conducted by some authors concerned about the relationship between variables of the human crania or head (length, breadth, cranial index or cephalic index) and body size (length of the lower limbs or body stature) gave conflicting results e.g., that maximum cranial length (GOL) changes in line with lower limb length, but not maximum cranial breadth (XCB)⁴⁸; or that the breadth of the head correlates directly with stature⁴⁹. Thus, the main problem is concerned with assessing which of the cranial shape changes can be explained by the result of secular change caused by changes in the quality and quantity of available nutrition⁴⁸. Unfortunately, in case of the individuals included in our study we did not have the opportunity to collect the measurements of their limb bones.

The results of our study indicate that variations in the cranial base breadth shows clear latitudinal gradient (in terms of temperature). In our opinion the occurrence of this regularity, despite other factors which could influence the size and shape of the neurocranium, can be interpreted as the result of long-standing mechanisms of climatic adaptation based on genetic factors. The mentioned above suggestion do not contradict the assertions that cranial base is a phylogenetically conservative structure. We think that (see the results of Roseman's research¹²) natural selection can be regarded as a main factor which shaped the inter-population differences in the cranial morphology. It means that the individuals less »adjusted« to the environment (e.g. in the case of colder climate, individuals with less globular heads than others,

thus with lower values of basicranial breadth) were »eliminated«. As a result of this process we can observe greater inter-population than intra-population differences in the basicranial breadth.

The results of our study suggest that the breadth of the cranial base can play a key role the mechanism underlying human adaptation to climate. The cranial base is more important for the growth and development of the whole cranium than other regions of the skull. The integration between the major parts of the skull is expressed through covariation between breadths of the traits (e.g., cranial base, cranial vault and the face)²⁷ and can determine their evolutionary response; thus, a change in basicranial breadth can induce changes in the shape of the cranial vault and face. This integration may enhance the evolution of cranial morphology towards a shape change that reflects adaptation to the ambient temperature. It is highly probable that brain growth during development also plays an important role in the mechanism of cranial adaptation to climate. The breadth of the brain influ-

ences the breadth of the middle cranial fossa³², and, as Lieberman et al.³¹ showed, endocranial volume and maximum basicranial breadth together account for 56% of the variation in maximum cranial vault breadth in modern human crania from diverse geographic regions. Our suggestion that ambient temperature contributes to the observed differences in skull basicranial breadth in modern humans should be tested further. The interesting issue of whether our observations in modern humans will be also visible in fossil *Homo sapiens* crania and other hominins (e.g., Neanderthals) is still unknown.

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MORFOLOŠKA PRILAGODBA LUBANJE HOMO SAPIENSA KLIMATSKIM UVJETIMA: VAŽNOST BAZOKRANIJALNE ŠIRINE

S A Ž E T A K

Cilj ove studije je istražiti povezanost varijabilnosti širine baze lubanje i klimatskih adaptacija kod modernih ljudskih populacija koje nastanjuju različite regije svijeta, na temelju preispitivanja dvije hipoteze. Prva hipoteza pretpostavlja da je korelacija između bazokranijalne širine i temperature okoliša jača od korelacije između temperature i drugih neurokranijalnih varijabli kao što je maksimalna širina lubanje, maksimalna neokranijalna dužina, endokranijalni volumen itd. Druga hipoteza smatra da je korelacija između širine baze lubanje i temperature okoliša značajna čak i kada su druge neurokranijalne varijable uključene u studiju, uključujući i veličinu neurokranijuma, konstantne. Za potrebe ovog istraživanja, prikupljene su bitne neurokranijalne varijable iz Howellovih podataka (sve osim podataka o endokranijalnom volumenu koji su dobiveni metodom procjene). Temperatura okoline (ili točnije, prosječna godišnja temperatura) u kojoj obitavaju ove populacije korištena je kao glavni klimatski faktor. Podaci su obrađeni koristeći Pearsonove koeficijente korelacije, linearnu regresiju i parcijalnu korelacijsku analizu. Rezultati podupiru obje hipoteze i impliciraju da temperatura okoline može utjecati na uočene razlike u širini baze lubanje kod proučavanih modernih ljudskih populacija.