БИОЛОГИЧЕСКАЯ АНТРОПОЛОГИЯ
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# TOWARD A NON-CONTRADICTORY EXPLANATION OF THE CLIMATE-RELATED VARIATION OF THE NASAL CAVITY AND MID-FACE

**Introduction.** *While the "Thomson-Buxton rule" describing the association between climate and the shape of the nasal aperture, and the nasal cavity in general, has been consistently confirmed at the global level, more detailed analyses at lower geographic scales reveal somehow contradictory results. The aim of this review was to summarize published data on the ecogeographic trends for the external and internal parts of the nasal cavity and mid-face in order to formulate a set of non-contradictory principles of the climate-related variation of these structures.*

**Materials and methods.** *All the publications on the subject written in English and Russian languages were considered with an emphasis on the recent works on North Eurasian samples that employed uniform protocols and were concerned with both external and internal aspects of the respiratory part of the facial skeleton.*

**Results and discussion.** *Proportions of the anterior nasal cavity are more important than its height and width separately. An increase in the total length of the nasal cavity might be achieved by both increasing nasal protrusion and by sagittal lengthening of the maxilla, but a strong nasal protrusion is a disadvantageous trait in frosty climates. The shape and surface area of the internal nasal cavity are more important than its total volume.*

**Conclusion.** *Most of the apparent contradictions between different studies on the ecogeographic variation of the facial skeleton can be reconciled by applying the concept of homoplasy, or convergent evolution: similar functional outcomes in morphologically distinct populations might be achieved via different morphogenetic mechanisms.*

**Keywords:** human climatic adaptation; cranial morphology; North Eurasia; respiratory physiology

## Introduction

The association between craniofacial morphology and climate has been studied for over a century [Thomson, 1913; Thomson, Buxton, 1923; Davies, 1932] at various geographical levels [Evteev et al., 2014, 2017; Bernal et al., 2014; Fukase et al., 2016; Menendez et al., 2017] but mainly using worldwide samples [e.g., Roseman, 2004; Harvati,Weaver, 2006; Noback et al., 2011; Maddux et al., 2016, among many others]. At a global level, the "Thomson-Buxton rule" formulated more than a hundred years ago has been consistently confirmed: populations from colder and drier climates demonstrate a relatively taller and narrow nasal aperture and/or nasal cavity in general. This apparent correlation finds very sound support in the laws of respiratory physiology [Cole, 1982 and Franciscus, 1995; Maddux et al., 2016 for a review]. In fact, even the earliest works were based on the theoretical background quoted from physiology, comparative anatomy and medicine [Thompson, Buxton,

1923, p.92; Davies, 1932, p. 349]. Briefly, a narrow nasal aperture decreases the velocity of inhaled airstream providing more time for air-conditioning inside the nasal cavity, or for retaining heat and water during expiration. A narrow and "tight" cavity, in turn, facilitates the contact between the air and the mucosa which leads to better warming and moistening. A compromised ability of the nasal cavity to condition the air leads to severe health outcomes [Franciscus, 1995].

But more detailed analyses at lower geographic levels reveal somehow contradictory results. For instance, the worldwide studies convincingly describe the inhabitants of high latitudes as displaying large, wide and flat faces [e.g. Roseman, 2004; Noback et al., 2011; Stansfield et al., 2021] while the works limited to West Eurasia and Africa show that populations from relatively cold-dry climates display a narrower face and a strongly protruding nose [Carey, Steegmann, 1981; Franciscus, 1995]. Relatively little is known about the ecogeographic variation of the internal part of the nasal cavity playing the most important role in air-conditioning [e.g. Cole, 1982; Keck et al., 2000]. Most previous studies were either employing limited samples or only indirectly assessing form of the internal cavity [Yokley, 2009; Butaric et al., 2010; Holton et al., 2013; Butaric, 2015; Butaric, Maddux, 2016; Maddux, Butaric, 2017]. During the last years, substantial samples of CT scans of modern and some ancient Eurasian populations have been studied from the point of view of the ecogeographic variation of the size and shape of the internal nasal cavity employing a uniform protocol [Evteev, Grosheva, 2019; Manakhov, 2022].

Thus, the aim of this review is to summarize published data on the ecogeographic variation of the external and internal parts of the nasal cavity and mid-face with an emphasis on North Eurasian groups and to formulate a set of non-contradictory principles of the climate-related variation of these structures.

## Material and methods

The main aim of the present inquiry is to reconcile some contradictions existing in the field and to formulate some simple and universal principles applicable to explaining most of the apparent climate-morphology associations observed in ancient and modern hominins. Thus, all the publications on the subject written in English and Russian languages were considered [see Evteev, 2021 for a review] but mainly those displaying apparent contradictions in their outcomes. The core of the study is the recent publication of the author and his colleagues based on North Eurasian samples, employing uniform protocols, and concerned with both external [Evteev et al., 2014, 2017] and internal [Evteev, Grosheva, 2019; Manakhov, 2022] aspects of the respiratory part of the facial skeleton.

The concept which inspired the search for such universal principles is homoplasy or convergent evolution: the achievement of a similar functional effect via different morphogenetic mechanisms [Severtsov, 2005].

## Results

### *Proportions of the anterior nasal cavity are more important than its height and width considered separately*

This conclusion may seem trivial as the very first works on the subject revealed the highest correlations with climatic variables for the nasal index, not single dimensions of the piriform aperture [Thomson, Buxton, 1923]. But as modern analytical techniques (e.g. partial least squares analysis, PLS) treat separate variables rather than their indices, apparent controversies might emerge. In fact, numerous studies have revealed very stable negative correlations between nasal height and temperature [see Franciscus, 1995 and Maddux et al., 2017 for a review], including our own recent work on Asian data [Evteev, Grosheva, 2019]. Thus, the absolutely low nasal aperture and cavity in cold-adapted Northeastern Europeans [Evteev et al., 2017; Manakhov, 2022] was a finding apparently contradictory to the bulk of existing knowledge. But it is worth noting that very similar proportions of the nasal cavity (or piriform aperture) can be achieved

despite completely different absolute dimensions (fig. 1). In this example, the Yakuts from Siberia exhibit a substantially taller (6.5%) and wider (10%) anterior nasal cavity than the Finns, but the ratio between the width and height of the anterior nasal cavity displays only a difference of 3.3%. Thus, in some human groups (e.g. modern North Asians or European Neanderthals [Franciscus, 1995]) the anterior nasal cavity can remain absolutely wide while relatively narrow due to an increase in height. In Neanderthals, narrowing is further emphasized by characteristic outgrowths at the internal margins of the nasal aperture [Schwartz et al., 2008]. But in other populations (e.g. the Paleolithic modern humans [Stansfield et al., 2021] from Europe or West Eurasians [Manakhov, 2022] from cold climatic zones) the same effect is achieved through a substantial absolute narrowing of the cavity accompanied by a decrease in height [see Hubbe et al., 2009 and Butaric, Klocke, 2017 for a similar discussion].

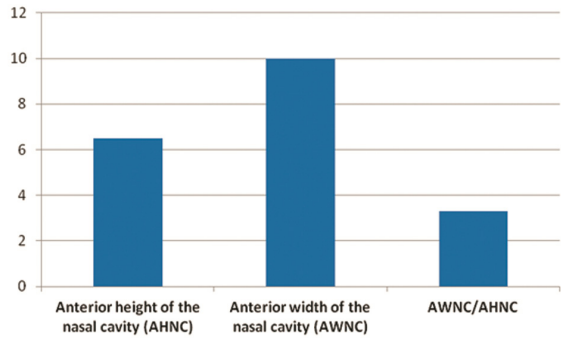


*Figure 1. Differences (in percent) between the Yakuts and Finns in the anterior width and height of the nasal cavity and their ratio*
*Рисунок 1. Отличия (в процентах) между якутами и финнами по ширине и высоте передней части ноовой полости, и по их соотношению*

*An increase in the total length of the nasal cavity might be achieved by both increasing nasal protrusion and by sagittal lengthening of the maxilla*

Numerous studies show the association between the total anteroposterior length of the nasal cavity with climatic conditions in various regions and at various geographic scales [Franciscus, 1995; Noback et al., 2011; Evteev et al., 2014, 2017; Fukase et al., 2016; Evteev,Grosheva, 2019]. But, clearly, two different morphogenetic phenomena can contribute to the total elongation: an increase in the nasal protrusion and an increase in the sagittal length of the body of the maxilla, the bone housing the main part of the functional nasal cavity. An example is given in Figure 2. The Buryats from South Siberia and Ossetians from the North Caucasus display nearly identical total lengths of the cavity but the contribution of the nasal protrusion to the length is almost twice as large in the Ossetians. Selection in various populations might operate on either of these mechanisms, or both. The increase in nasal protrusion is typically observed in West Eurasians [Carey, Steegmann, 1981; Franciscus, 1995], except Northeastern Europe, while lengthening of the maxilla is mainly found in North Asia. In some groups, both mechanisms might be operating, e.g. in European Neanderthals exhibiting a large facial skeleton in combination with a strong nasal protrusion [Franciscus, 1995], or the Bronze age sample from Ginchi [Manakhov 2022] in which both components of the total length of the cavity are fairly developed.

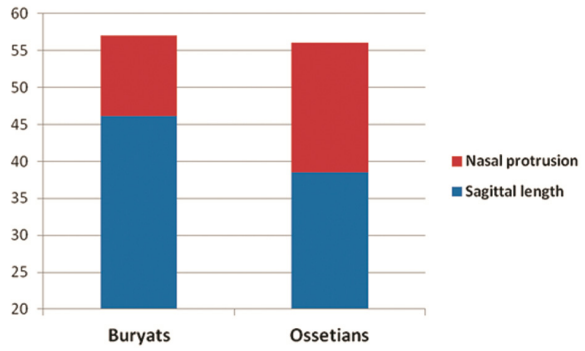


*Figure 2. Partitioning of the total length of the nasal cavity in the samples of the Buryats and Ossetians.*
*Рисунок 2. Компоненты общей длины носовой полости у бурят и осетин*

Notes. Y-axis represents the values of the variables in mm.

Примечания. По оси Y отложены абсолютные значения признаков в мм.

*A strong nasal protrusion is a disadvantageous trait in frosty climates*

Of the two mechanisms of lengthening the nasal cavity outlined in the previous section, the increase in the nasal protrusion plays a minor role in high latitude groups, in other words, in the populations inhabiting areas experiencing long frosty periods during winter. Moreover, a flattening of the nasal bridge and external nose (or at least an absence of an increase in nasal protrusion) is consistently observed in the groups from boreal areas of Europe [Evteev et al., 2017; Manakhov, 2022], Asia [Woo, Morant, 1934; Evteev et al., 2014], and the Americas [Hrdlička, 1910; Hylander, 1977; Hernández et al., 1997; Menendez et al., 2021]. As it has been demonstrated for West and East North Eurasians [Evteev et al., 2014, 2017; Evteev, Grosheva, 2019; Manakhov, 2022], this is compensated by an increase in anteroposterior length of the maxilla through which a total lengthening of the cavity is achieved. A possible explanation for this observation is the higher risk of freezing of the external nose in those regions [see Franciscus, 1995 for a review of related medical literature].

The alternative mechanism of lengthening of the nasal cavity is present in the populations of the temperate zone of Europe, the Mediterranean, and the Caucasus that exhibit a strong nasal protrusion and, as a result, a long nasal cavity despite a relatively anteroposteriorly short maxilla. Such a combination contrasts them with both populations from the south (i.e. Sub-Saharan groups) and north (i.e. Northeastern Europe).

*The shape and surface area of the internal nasal cavity are more important than its total volume*

The trends for the volume of the nasal cavity in West [Manakhov, 2022] and East [Evteev,Grosheva, 2019] North Eurasia are directly opposite, thus corroborating the previously expressed idea that the shape of the nasal cavity might be more important from the ecogeographic point of view than its total size [Noback et al., 2011; Fukase et al., 2016; Maddux et al., 2017]. The role of the nasal mucosa and turbinates in determining the functional volume of the cavity [Heuzé, 2019; Marks et al., 2019; Marechal et al., 2022] should not be overlooked, and this cannot be directly assessed in skeletal specimens.

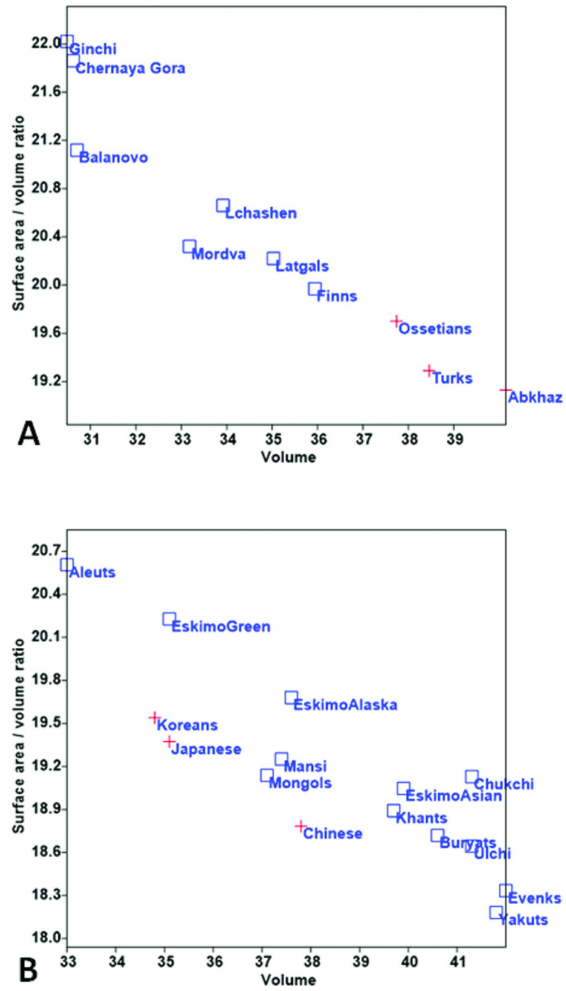


*Figure 3. Linear regression of the surface area to volume (SA/V) ratio on nasal cavity volume. A – West Eurasia; B – East Eurasia and Arctic*
*Рисунок 3. График линейной регрессии индекса поверхность / объем к объему носовой полости. А – европеоидные группы; Б – монголоидные группы*

Notes. Blue squares – cold-adapted groups, red crosses – temperate climate groups. Volume of the nasal cavity – in $cm^3$.

Примечания. Голубые квадраты – обитатели холодного климата, красные кресты – обитатели умеренного климата. Объем носовой полости указан в $см^3$.

The total volume might be to a substantial degree a function of the total size of the facial skeleton [Butaric et al., 2010; Fukase et al., 2016; Evteev, Grosheva, 2019]. At the same time, the surface to volume ratio of the cavity (SA/V), as was expected as well [Franciscus, 2003; Yokley, 2009], display more interpretable associations with climatic conditions. According to the results of our recent

research, cold-adapted groups from West Eurasia, both modern and ancient, displays a higher SA/V ratio than the groups from warmer climates (fig. 3a). The trend is less straightforward in populations of Asian descent [Evteev, Grosheva, 2019; fig. 3b]. Most of the cold-adapted groups display enlarged volumes and reduced SA/V, but at a given volume this ratio in the North Asian and Arctic populations is higher than in the East Asian groups: compare the Koreans and Japanese vs. Greenlandic Eskimo, and the Chinese vs. Mansi, Mongols and, in particular, Alaskan Eskimo. Thus, a decrease in the volume of the nasal cavity in high latitudes of North Eurasia is not accompanied by a proportional decrease in its surface area due to the changes in the shape of the cavity.

## Conclusion

Most of the apparent contradictions between different studies on the ecogeographic variation of the facial skeleton can be reconciled by applying the concept of homoplasy, or convergent evolution: similar functional outcomes in morphologically distinct populations might be achieved via different morphogenetic mechanisms. Thus, a particular shape of the nasal aperture and anterior nasal cavity can be the result of various combinations of their height and width, and additional structures of the lateral walls should be taken into account as well. The length of the nasal cavity can be determined by both the degree of nasal protrusion and the size of the body of the maxilla. The surface area to volume ratio is increased in high-latitude populations of both West and East Eurasia but this increase can be either absolute or relative.

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# ОПЫТ ОБОБЩЕНИЯ ДАННЫХ ОБ ЭКОГЕОГРАФИЧЕСКОЙ ИЗМЕНЧИВОСТИ НОСОВОЙ ПОЛОСТИ И ЛИЦЕВОГО ЧЕРЕПА: СУЩЕСТВУЮЩИЕ ПРОТИВОРЕЧИЯ И ИХ ВОЗМОЖНЫЕ РЕШЕНИЯ

**Введение.** *Основные закономерности взаимосвязи между формой носового отверстия (и носовой полости в целом) и климатическими показателями, иногда называемые «правилом Томсона-Бакстона», были установлены более 100 лет назад. Последующие исследования, особенно проведенные на глобальном уровне, неизменно подтверждали это правило, однако более детальные работы на континентальном или локальном уровнях давали в некоторых случаях противоречивые результаты. Целью данного обзора было «примирить» эти противоречия, и сформулировать ряд принципов, универсально применимых для объяснения наблюдаемых корреляций морфологии лицевого черепа и климата.*

**Материалы и методы.** *Привлекались все имеющие отношение к рассматриваемому вопросу источники на русском и английском языках. Особое внимание было уделено данным по Северной Евразии, полученным в последние годы автором и его коллегами с применением единого протокола исследования как наружных, так и внутренних структур лицевого черепа.*

**Результаты и обсуждение.** *Пропорции передней части носовой полости имеют большее значение, нежели ее высота и ширина, рассматриваемые по отдельности. Увеличение общей сагиттальной длины носовой полости может достигаться как за счет усиления выступания носа, так и за счет увеличения длины непосредственно тела верхнечелюстной кости. Однако сильное выступание носа, по всей видимости, не является адаптивно благоприятным признаком в областях с холодным климатом. Форма и площадь поверхности внутренней носовой полости являются более важными показателями, чем ее общий объем.*

**Заключение.** *Большинство кажущихся противоречий между результатами отдельных исследований экогеографической изменчивости лицевого отдела черепа могут быть сравнительно легко устранены с помощь последовательного применения принципа конвергентной эволюции: формирование одинаково эффективных с точки зрения респираторной функции структур может происходить в разных популяциях с помощью различных морфогенетических механизмов.*

**Ключевые слова:** климатическая адаптация; морфология черепа; Северная Евразия; физиология дыхания

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