Restudying variations of axial skeleton patterning in Eskimo groups with new data from ancient Chukotka (Ekven archaeological site)

Marina K. Karapetian[1], Sergey V. Makarov[2]

[1]*Research Institute and Museum of Anthropology, Lomonosov Moscow State University, Moscow, Russia, Research Centre for Medical Genetics, Moscow, Russia*

SUMMARY

This study continues a series of studies by Stewart and Merbs on vertebral column variations in Eskimo groups. The focus is on so called craniocaudal shifts in spine patterning. The study is performed on a skeletal sample of ancient Eskimos from Siberia (Ekven site, Chukotka) and comparative samples representing population groups of European and African ancestry. In addition to these, literature data are used for comparative analysis to assess the pattern of cranio-caudal border shifts on intra-specific level. The result confirms the presence of significantly increased predisposition of the Eskimos to caudal shifts in spine patterning, expressed both as increased frequencies of complete caudal shifts of thoraco-lumbar and lumbo-sacral borders, as well as minor variations in vertebrae morphology, including variation in the type of articular processes (thoracic/lumbar types) and the position of costo-central articulation at T9 level. Hypotheses explaining this specific character of the Eskimo/Inuit groups are proposed and explored, including gene drift, influence of environmental factors and association with morphological characteristics adaptive to survival in the Arctic. One of the explanations may be the association with characteristic form and size of the thoracic cage that distinguishes the Arctic groups such as Eskimos and Chukchi from groups leaving in more southern areas. This needs to be tested on other groups, living in similar conditions.

INTRODUCTION

Numerical variations of spine formula in humans and in non-human primates have long been a subject of biological and medical interest. First, because of their association with phylogenetic changes in locomotion pattern, thus interest in paleoanthropological studies (Todd, 1922; Schultz, 1930; Williams et al., 2016; Thompson and Almécija, 2017). Second, because of their inheritability (Kühne, 1932; Schapera, 1987) and, thus, interest in populations studies (Shore, 1930; Stewart, 1932; Lanier, 1939; Allbrook, 1955; Bornstein and Peterson, 1966; Tulsi, 1972; de Beer Kaufman, 1974; Merbs, 1974; Jankauskas, 1988). And, third, because of their presumed clinical significance and association with mutations and developmental anomalies (Galis et al., 2006; ten Broek et al., 2012; Nakajima et al., 2014; Tague, 2018).

The pattern of the axial skeleton is determined during prenatal development. When a shift in vertebra identity is observed at the border between two regions, this represents so-called homeotic transformation. It was shown that homeotic transformations along the axial skeleton may be associated with mutations in certain genes responsible for body patterning (e.g. *HOX* genes) (Mallo et al., 2010). In addition to genetic factors, possible impact of external factors, influencing the expression of genes during embryogenesis, is suggested from the experimental studies on animal models (e.g.

Corresponding author: Marina Karapetian. Mokhovaya str. 11/1, Moscow 125009, Russia.

E-mail: marishkakar@hotmail.com

Murakami and Kameyama, 1963; Chernoff and Rogers, 2004). That some homeotic shifts may represent deviations from normal development is suggested from studies, showing existence of significant prenatal/early postnatal selection of individuals with cervical ribs and association of cervical ribs with malformations in other organ systems (Schumacher et al., 1992; Galis et al., 2006; ten Broek et al., 2012).

Prehistory of the Eskimo/Inuit groups. The first representatives of the Eskimos (Paleo-Eskimos) appeared in Siberia; and about 5-6 thousand years ago they expanded into Alaska, eventually populating Canadian Arctic and Greenland. Later, Pale-Eskimo were replaced by the Neo-Eskimo (or Inuit) who are the direct ancestors of the modern Eskimo/Inuit groups. The earliest representatives of the Neo-Eskimo are found in Siberia, and in Alaska they first appear as carriers of the early Old Bering Sea culture at the turn of our era. The Thule culture (the direct ancestors of the modern Eskimo/Inuit groups in North America) emerged in Alaska about 1000 AD and expanded throughout the North American Arctic, replacing all Paleo-Eskimo groups living there. The Paleo-Eskimo cultures completely disappear in Alaska at about 800 AD and in Canada and Greenland at about 1300 AD (Raghavan et al., 2014; Friesen and Mason, 2016). Genetic evidence shows continuity in Paleo-Eskimo groups during more than 4000 years of occupation, and discontinuity between Paleo- and Neo-Eskimo groups of North America suggesting incident of population replacement (Raghavan et al., 2014).

Study background. In the early 1930s Stewart presented his detailed observations on the Eskimo spine when he worked with skeletal remains brought by Ales Hrdlička from Alaska (Stewart, 1932). Notably, he pointed to an apparently high prevalence of caudal border shifts at lumbo-sacral border, e.g. elongated pre-sacral spine (25 vertebrae), with no cases of the shortened pre-sacral spines (23 vertebrae). High prevalence of individuals with 25 pre-sacral vertebrae relative to other population groups was also observed on a sample of Sadlermiut Eskimos from Southampton Island (Merbs, 1974) and on a pooled sample of Native Americans (including Koniag Eskimos, Aleutians and Plain Indians) (Borstein and Peterson, 1966). Lanier, in his detailed study on pre-sacral spine variations in American Whites and Blacks, while performing comparison with other population groups using literature sources, noted that caudal type variations are most frequent in Eskimo group (Lanier, 1939).

Unfortunately, no analogous studies were performed on the Asian Eskimos, who are closely related both genetically and by living conditions to the groups from Alaska and North Canada. Thus, it is not known to what extent the morphological specificity observed for the American Eskimo/Inuit groups are characteristic for this circumpolar population as such, and thus might represent a very ancient morphological complex.

At the Asian part of the Beringia, one of the most outstanding ancient sites is the Ekven burial site. The site was located on the far east point of Chukotka near Cape Dezhneva. Most burials belong to the Old Bering Sea (I–III) and Okvik cultures, embracing the period from about the end of the 1st millennium BC to the beginning of the 2nd millennium AD (Arutyunov and Sergeev, 1975; Friesen and Mason, 2016). Regardless of the wide temporal range, during which the burial ground functioned, craniological studies showed high level of homogeneity in metric traits, indicating the conservation of the anthropological type, well adapted to the extreme environmental conditions (Alexeeva et al., 2008).

The aim of this report was to assess frequencies of numerical variations of spine formula in Eskimo group from the Ekven site, as well as from Alaska and Canada, to perform a comparative analysis with other population groups using original data and data from the literature, and to test that Eskimos indeed show a strong tendency towards caudal shifts in pattern by studying minor variations of vertebrae morphology. Hypotheses explaining this morphological specificity of the Eskimo spine are proposed and explored.

MATERIALS AND METHODS

The Ekven Eskimo collection was studied in the Research Institute and Museum of Anthropology of the Lomonosov Moscow State University. Totally, 59 individuals were studied (30 males and 29 females). All except 7 individuals were adults (≥18 years). The 7 individuals were juveniles older than 14 years of age for whom sex could be estimated. They were studied to increase the sample size, and their inclusion is justified because by the age of 14 all key structures needed to identify the type of a vertebra are formed and synostosed (see Schaefer et al., 2009). The first and the second sacral segments may not fuse completely until the age of 25. However, partial union is usually present by puberty and, even if the fusion did not begin, the 1st sacral segment is identifiable based on its morphology (see Schaefer et al., 2009). Sex was estimated based on pelvic morphology according to criteria summarized by Buikstra and Ubelaker (1994). Age was estimated as Juvenile and Adult based on the degree of epiphyseal fusion (Schaefer et al., 2009).

In addition to the Ekven sample (Ekv), comparative samples representing population groups of different ancestry were studied: Russian (2 samples, Moscow region) (Rus); North American residents of European ancestry (samples from the Terry and Grant collections) (NA Eur); North American residents of African ancestry (sample from the Terry collection) (NA Afr). Samples studied by the authors are listed and described in Table 1. All individuals in these samples were adults.

Ekven sample and the three comparative samples were reviewed for the following traits:

1) Number of cervical (C), thoracic (T) and lumbar (L) vertebrae and the total number of pre-sacral vertebrae (PCV). Thoracic and sacral vertebrae were identified following classical criteria (Schultz, 1930), used in the overwhelming majority of studies. Following the costal criteria, a vertebra was identified as thoracic if it carried rib facet that indicated presence of articulation with a true rib. If a vertebra carried facet only on one side, it was also considered thoracic. The 24th vertebra was considered sacral if it was fused (non-pathologically, unilaterally or bilaterally via lateral masses) to the sacrum. The 25th vertebra was considered pre-sacral (lumbar) if it was completely separated from the sacrum and articulated with it only via joint facets (in some cases also via extra facets on the enlarged transverse processes) (Lanier, 1939; Jankauskas, 1988). The number of vertebrae was recorded only when this was certain. For example, 11 thoracic vertebrae were scored only when there was no indication of post-mortem loss of one thoracic vertebra (all present vertebrae were congruent with adjacent vertebrae); and the same was done for the cervical and lumbar spines. If spine formula differed from the modal (7C-12T-5L), a presence of border shift was stated (cranial – towards the cranium; caudal – towards the coccyx).

2) Position of transitional vertebra at T-L border – lowermost vertebra with superior articular processes of thoracic and inferior articular processes of lumbar type. Thoracic type superior ar-

ticular processes were scored when they were oriented dorsolaterally; lumbar type were scored when they were oriented dorsomedially; and vice versa for the inferior articular processes (after Lanier, 1939). If articular facets were asymmetrical, e.g. left superior facet of T12 was thoracic-type and right was lumbar-type, then 0.5 of this individual had transitional vertebra at T12 level (left side) and another 0.5 – at T11 level (right side).

3) Presence of any **signs of cranial/caudal shift in spine patterning** at C7, T9 (shift in the position of the last typical thoracic vertebra), T10 (shift in the position of the last vertebra articulating with rib tubercle), T12, L1, L5 and S1 according to criteria, summarized in Table 2. Statement of shift in T9 and T10 morphology proceeded from the customary anatomical description of these vertebrae (Gray, 1858).

The resulting data on the 1st group of traits (cranio-caudal border shifts) were combined with the literature data. First the data on the Asian, Alaskan and Canadian Eskimo groups were combined to compare trait distribution in different Eskimo samples. Then data on Eskimo groups were compared with data on other population groups to assess the extent of specificity of these groups relative to populations from other geographical areas. Fig. 1 illustrates geographical origin of Eskimo samples analyzed in this study. Unfortunately, Borstein's and Peterson's data on Koniag Eskimos, presented in their article (Borstein and Peterson, 1966), could not be included here, because

Table 1. Description of samples studied by the authors.

Sample description	Collection	Geographic origin	Sampling strategy	Sex assessment	Chronology	N Males	N Females
Ancient Eskimos	Ekven, Research Institute and Museum of Anthropology, Lomonosov Moscow State University	Chukotka	All adults and all juveniles (>14 years) with estimable sex and with spine present	Estimated[a]	Old Bering Sea/Okvik culture	5 juveniles and 25 adults	2 juveniles and 27 adults
USA residents, European descent	Terry, National Museum of Natural History, Smithsonian Institution	Missouri, USA	Random within sex group	Known	1924-1966	72	70
USA residents, African descent		Missouri, USA	Random within sex group	Known	1932-1966	35	37
Ontario residents, European descent	Grant, University of Toronto	Ontario, Canada	All females; males randomly	Known	1931-1950	84	21
Moscow residents (anatomical collection)	Anthropology Department, Lomonosov Moscow State University	Moscow, Russia	All adult individuals	Estimated[a]	1950th	66	14
Kozino village cemetery	Research Institute and Museum of Anthropology, Lomonosov Moscow State University	Moscow region, Russia	All adult individual with complete spine	Estimated[a]	18th C.	78	53

[a]Based mainly on pelvic morphology but taking into account the standard criteria for the cranium (Buikstra, Ubelaker, 1994)
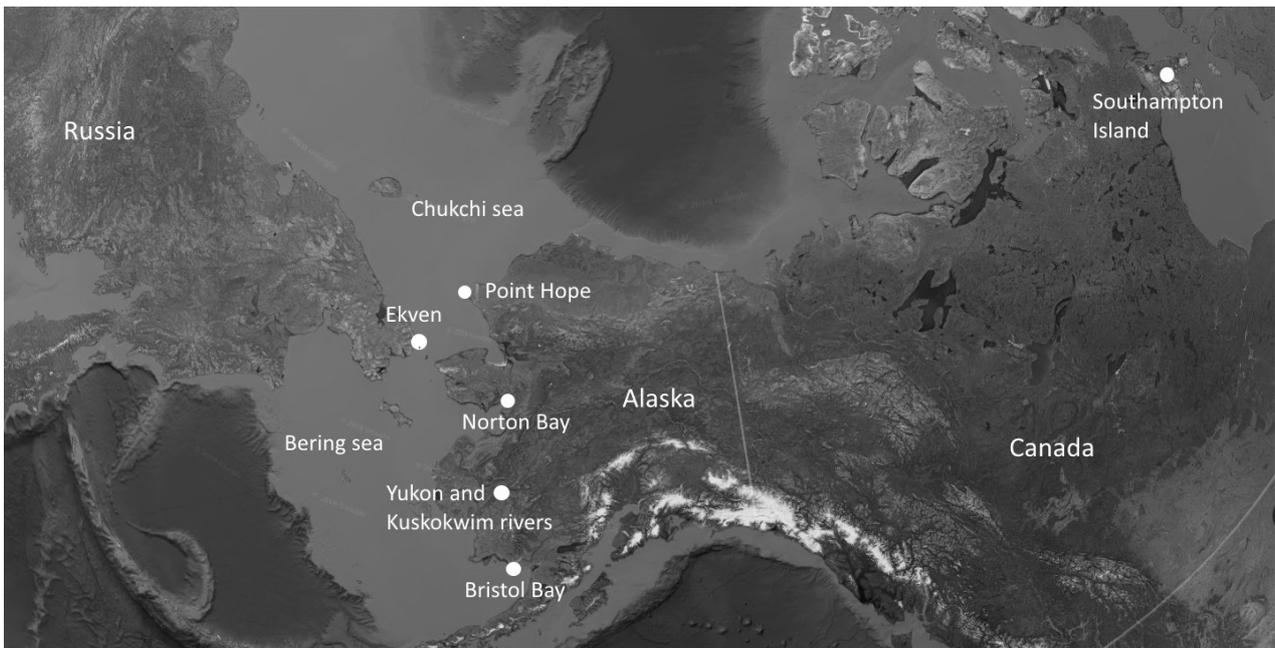
Fig 1. Geographical origin of the Eskimo samples analyzed (white dots). Alaskan sample includes remains from Point Hope, Norton Bay, Bristol Bay, Yukon and Kuskokvim river regions studied by Stewart (1932); Eskimo remains from Southampton Island were studied by Merbs (1974) (drawing based on www.google.com/maps).

Table 2. List of traits used as signs of cranial/caudal shift in spine patterning.

Level	Cranial shift	Caudal shift	No shift
C7	Costal processes of C7 are markedly enlarged or are developed into cervical ribs	Transformation of T1 into C8 (no 1st ribs)	C7 typical, 1st ribs develop at T1 level
T9	-	Presence of both superior and inferior rib facet on the vertebral body[a]	T9 has only superior rib facets on the body (10th rib articulates only with T10)
T10	No rib facets on transverse processes of T10[a]	-	T10 have rib facets both on the body and on the transverse processes (10th rib articulated both with the body and with the transverse process)
T12-L1	No rib facets on T12 (11 thoracic vertebrae) and/or T12 has superior articular processes of the lumbar type[a]	L1 develops rib/ribs (13 thoracic vertebrae) and/or has superior articular process of thoracic type[a]	19th vertebra has superior articular processes of thoracic type and inferior of the lumbar type, articulates with the 12th pair of ribs; 20th vertebra has superior articular processes of lumbar type and has normally developed transverse processes, no ribs present at L1 level
L5-S1	24th vertebra is assimilated by the sacrum or has markedly enlarged transverse processes assuming the form of the sacral vertebra	S1 approaches the form of lumbar vertebra with complete separation from S2	24th vertebra is usual; S1 is fused (or in a process of fusion) to S2

[a]The shift is stated both in cases of unilateral and bilateral appearance

they were pooled with Aleutian and Plain Indian samples. Alaskan samples are pooled in two: North (Point Hope and Norton Bay) and South (Yukon and Kuskokwim rivers, Bristol Bay) after Stewart (1932).

The second and third group of traits were analyzed using only samples studied by the authors. Tests for statistical differences were performed using χ2-test (for nominal data) and Mann-Whitney U-test (for ordinal data). All computations were performed in STATISTICA program (v. 8) (StatSoft, 2007).

RESULTS

The resulting data on occurrence of vertebral border shifts (1st group of traits) in the Eskimo groups are presented in Table 3. Overall, the Ekven sample shows characteristics similar to the Eskimo groups from Alaska and Southampton Island, i.e. predominantly caudal shifts both at T-L and L-S borders with practically absent cases of cranial shifts at all three borders (C-T, T-L, L-S). Note that both the Ekven sample and the Alaskan samples do not have cases of numerically shortened spines (23 PCV) and cases of shortened tho-

Table 3. Frequencies of cranial/caudal shifts at C-T, T-L, L-S borders in four Eskimo/Inuit samples from Siberia and North America[a].

Group	Data source	Cervical ribs (6 C vertebra)				Reduction of 12th pair of ribs				Presence of ribs at L1 level				L5 assimilated (23 PCV)				S1 separated (25 PCV)				Mean % variation
		M	N	F	N	M	N	F	N	M	N	F	N	M	N	F	N	M	N	F	N	
Ekven	This study	0	14	0	12	0	30	0	29	2	29	1	27	0	25	0	23	4	24	2	23	3.6
Alaska North	Stewart, 1932	0	38	0	23	0	38	0	23	5	38	0	23	0	38	0	23	8	38	0	23	4.2
Alaska South	Stewart, 1932	0	69	1	73	0	69	0	73	8	69	3	73	0	69	0	73	9	69	7	73	3.9
Sadlermiut	Merbs, 1974	0	33	0	37	1 out of 70				11 out of 70				0	33	2	37	4	33	2	37	5.7

[a]When possible, sex specific data is presented: M – Males, F – females, N – number of individuals

Table 4. Comparison of frequencies of individuals with 13 thoracic vertebrae and 25 presacral vertebrae in 4 Eskimo/Inuit samples (results of Chi-square test, both sexes) (based on data from Table 3).

	13 thoracic vertebrae			25 presacral vertebrae		
	Alaska North	Alaska South	Sadlermiut	Alaska North	Alaska South	Sadlermiut
Ekven	NS	NS	NS	NS	NS	NS
Alaska North	-	NS	NS	-	NS	NS
Alaska South	-	-	NS	-	-	NS

Table 5. Comparing frequencies (%) of cranial (Cr) and caudal (Caud) shifts in spine patterning in four samples studied by the authors.

	N	C7-T1 Cr	T9 Caud		T10 Cr	T12-L1		L5-S1		Mean variation	
			Males	Females		Cr	Caud	Cr	Caud	Cr	Caud
NA Eur	237	**5.1**	**59.2**	**33.8**	**62.3**	39.5	6.9	9.1	6.6	29.0	26.6
Rus	182	**6.7**	**68.0**	**42.0**	44.9***	33.8	6.3	5.4	**3.4**	22.7	29.9
NA Afr	63	17.4***	**63.6**	**32.4**	46.4*	45.7**	7.0	7.2	**0.0**	29.2	25.8
Ekv	59	**0.0**	96.6***	76.9***	50.0	**23.7**	10.2	4.5	11.4**	19.6	48.8

The sample significantly differs at *p<0.05; **p<0.01; ***p<0.001 levels from samples marked with bold

racic spines (11 thoracic vertebrae), while in the Sadlermiut Eskimos there are few cases (2.9 and 1.4% respectively). Caudalwards shift of C-T border is extremely rare in humans and was not observed in any of the Eskimo groups. No statistical difference is observed between 4 Eskimo samples (Table 4), although the Sadlermiut sample shows slightly higher overall percentages of variations (Table 3).

Four samples, studied by the authors (Ekv, Rus, NA Eur, NA Afr), were used to analyze the variation of cranial/caudal shifts in spine patterning (3rd group of traits). Though there is a general tendency for females to have slightly higher frequencies of cranial shifts compared to males and vice versa for the caudal shifts, sex differences are significant only in isolated cases and the only trait that shows systematic and highly significant (<0.001) variation related to sex is the caudalwards shift at T9. Thus, to simplify the analysis, data for sexes were pooled, except for this trait which was analyzed separately for sexes. The results are presented in Table 5. Here distinct pattern is evident: the Ekven sample indeed shows significant predisposition to caudal shifts in patterning, especially against the

group of African ancestry, showing increased predisposition to cranial shifts. Interestingly, the caudal shift at T9 level is the trait that distinguishes most significantly the Ekven sample from samples of other population groups, both within males (97% in the Ekven sample and about 64% in others, p<0.001) and females (77% in the Ekven sample and about 36% in others, p<0.001). This is in striking contrast with the fact that other 3 samples do not show any significant variation in this trait, apart of that related to sex.

The mean position of transitional vertebra is slightly higher (more cranial) in females (18.7 vs 18.8 in males). However, sex difference is significant at 0.05 level only in one sample (NA Eur). The transitional vertebra most often is the 19th (T12), though in some cases it is the 18th (T11) and in rare cases the 20th (L1) (Table 6). Although this distribution is repeated in all samples, the mean position of the vertebra is shifted slightly caudal in the Ekven sample and this shift is significant (<0.05) compared to two samples out of three (18.9 in the Ekven vs 18.6-18.7 in North American samples of European and African ancestry).

To test if the predisposition towards caudal shift

in pattern at various spine levels in the Eskimo sample is a result of strong correlation between different unidirectional traits, the association between traits was studied. Percentages of co-occurrence was calculated for each pair of traits and compared to expected values, as if the traits were independent. First, this was done within each of the four samples. The only significant result was for the co-occurrence of caudal shift at T9 level and cranial shift at T-L border: the traits were found together significantly less frequently than it would be expected (in North American sample of European ancestry). The general results reveal only a slight degree of association which does not reach the level of statistical significance, because all unidirectional traits appeared systematically more often together, while all oppositely varying traits appear systematically less often together than it would be expected, given their independence. This pattern is repeated in all studied groups. The same pattern persists when all samples are pooled and analyzed according to sex (Table 7), and is illustrated in the Fig. 2. Thus, while traits do not seem to vary completely independently from each other, they are not strongly associated and may be studied as complementary sources of information.

An additional test was performed to see if the Ekven sample differs from other samples in the degree of traits' asymmetry: i.e. if the level of asymmetry in the Ekven sample is increased/ decreased in relation to other samples. As data in Table 8 shows, the Eskimo sample does not differ in any significant way from other studied groups of European and African ancestry. The most stable trait in terms of symmetry is the presence of inferior rib facet on the T9 body (caudal shift in patter of T9).

Appendix 1-4 presents compiled data (this study and literature sources) on cranial and caudal shifts

Table 6. Comparing differences in the position of transitional vertebra in four samples studied by the authors.

Sample	N	Position of transitional vertebra, %						Mean position of transitional vertebra		
		Males			Females			M	F	All
		18	19	20	18	19	20			
NA Eur	232	31.1	63.5	5.4	46.4	50.0	3.6	18.7	18.6	**18.7**
Rus	181	26.0	69.0	5.0	31.3	64.6	4.0	18.8	18.7	18.8
NA Afr	70	44.1	52.9	2.9	37.5	55.6	6.9	18.6	18.7	**18.6**
Ekv	57	21.7	68.3	10	18.5	77.7	3.7	18.9	18.9	18.9*
All	540	29.6	65.0	5.4	37.2	58.5	4.3	18.8	18.7	18.7

* This sample significantly differs from other samples (marked with bold) at 0.05 level

Table 7. Observed and expected (in brackets) percentages of co-occurrence of cranial (Cr) and caudal (Caud) shifts at various spine levels (pooled samples of males and females).

	T9 Caud	T10 Cr	T12-L1		L5-S1	
			Cr	Caud	Cr	Caud
Males (N=330)						
C7-T1 Cr	2.7(3.9)	3.9(3.3)	3.3(2.1)	0.0(0.4)	1.1(0.5)	0.0(0.4)
T9 Caud	-	28.6(34.6)	19.4(24.0)	6.1(4.8)	3.8(4.6)	4.4(3.3)
T10 Cr	-	-	22.0(19.8)	3.7(4.1)	4.5(4.1)	2.7(2.7)
T-L Cr	-	-	-	0.3(2.9)**	4.0(2.5)	0.6(2.0)
T-L Caud	-	-	-	-	0.3(0.6)	2.3(0.5)
L-S Cr	-	-	-	-	-	0.0(0.6)
Females (N=196)						
C7-T1 Cr	1.9(3.7)	7.1(5.1)	4.6(4.1)	0.0(0.6)	1.8(0.8)	0.0(0.4)
T9 Caud	-	16.2(20.5)	8.8(16.2)*	3.9(2.8)	1.2(3.2)	3.6(1.7)
T10 Cr	-	-	27.4(21.7)	3.3(3.8)	7.6(4.4)	1.3(2.0)
T-L Cr	-	-	-	1.0(2.6)	4.4(2.8)	0.3(1.7)
T-L Caud	-	-	-	-	0.0(0.4)	2.5(0.3)
L-S Cr	-	-	-	-	-	0.0(0.0)

* Difference between observed and expected frequencies significant at 0.05 level and
** at 0.01 level

of T-L and L-S borders in various human population groups. Distribution of C-T border shift was not analyzed here, as this variant is rare in most of the population groups. Trait frequencies were averaged for 4 ancestry groups for whom data on at least 3 independent samples are available: European ancestry (including Europe, European part of Russia and North America); African ancestry (including Africa and North America), Japanese and Eskimo. The resulting data was plotted against mean human frequencies and 95 confidence intervals for the mean, calculated using all samples from Appendix 1-4. The plot reveals the following general pattern of traits' variability at inter-population level (Fig. 3):

Eskimo groups on an average show markedly increased predisposition to caudal border shifts both at T-L and L-S borders, showing highest mean values for humans, while cranial border shifts are not characteristic for this population group. They also show slightly increased percentages of variations in spine formula compared to mean human values. However, this increase is solely due to higher percentages of anterior homeotic transformations (caudal shifts).

Groups of African ancestry also show slightly increased variability in vertebral formula (see also SD in tables from Appendix 1-4); on an average, they show increased predisposition towards cranial shifts at T-L and L-S borders;

Japanese are least variable in terms of vertebral formula (lowest averaged frequencies of both cranial and caudal border shifts);

The results generally confirm that Eskimo groups are indeed characterized by strong predisposition to caudal border shifts and numerical elongation of the pre-sacral spine on an intra-specific scale.

DISCUSSION

This article analyzes shifts in spine patterning expressed as minor variations in vertebrae morphology and as regional border shifts between cervical, thoracic, lumbar and sacral segments in a sample of ancient Eskimos from Siberia (Chukotka), in comparison to more recent Eskimo/Inuit samples from Alaska and Canada, reported previously in the literature (Stewart, 1932; Merbs, 1974), and to samples from non-Eskimo population groups. The Siberian Eskimos show similar morphological specificity as the Eskimo/Inuit groups from the American continent. Namely, both show a strong tendency towards caudal border shifts with decreased probability to develop cranial border shifts. Given the inherited nature of the shifts in spine patterning (Kühne, 1932), the similarities are likely due to close genetic affinity between all Eskimo populations. Because this specificity of the Eskimo spine is present both at Asian and American part of the Beringia and in Sadlermiut Inuit of Canadian Arctic, it likely developed very early, likely before the dispersal of the modern Eskimo/Inuit ancestors into Americas.
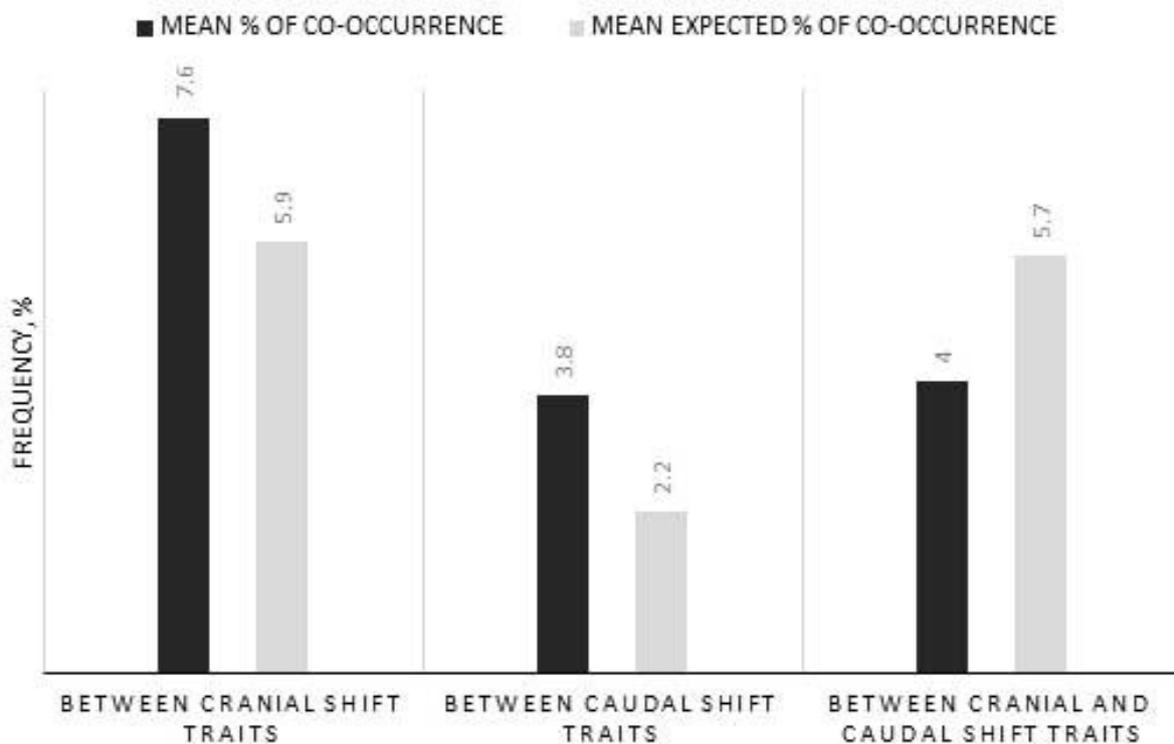
Of note is that the Sadlermiut sample is slightly

Fig 2. Mean frequencies of co-occurrence of the 3rd group of traits (based on data from Table 7) as compared to mean expected frequencies of co-occurrence of the same traits given that traits are not associated: unidirectional traits have relatively higher percentages of co-occurrence while oppositely directed traits tend to appear with each other less frequently than expected.

more variable on an average in terms of canio-caudal border shifts between spine regions compared to the Alaskan and Ekven samples. Merbs, in another study (2004), found a greater rate of expression of vertebral sagittal clefting – a rare developmental defect of the vertebral body - in a Sadlermiut sample, compared to a sample representing general Inuit population from Canadian Arctic. This, according to his view, could indicate genetic isolation of the small, likely more inbred Sadlermiut group. The higher proportion of close relatives within the sample would indicate that higher frequencies of developmental anomalies are expected.

The above discussed specifics of the Eskimo spine may be hypothetically related to the genetic drift in the ancestral population, which led to the increase in those allelic frequencies that are associated with anteriorization of vertebrae. However, it seems more likely that a strong tendency towards caudal shifts and elongation of the spine is a result of directional selection of genetic variants that are associated with characteristic body build of the Eskimos. For example, Eskimos have relatively longer trunk if compared, to groups from Sub-Saharan Africa – adapted to drastically different environmental conditions – who have lower ratio of limb to trunk length (Holliday and Hilton, 2010).

Table 8. Percentage of asymmetry in four bilateral traits: inferior rib facets on the T9 body, rib facets on the T10 transverse processes, orientation of superior articular facets (thoracic or lumbar type) on T12 and L1.

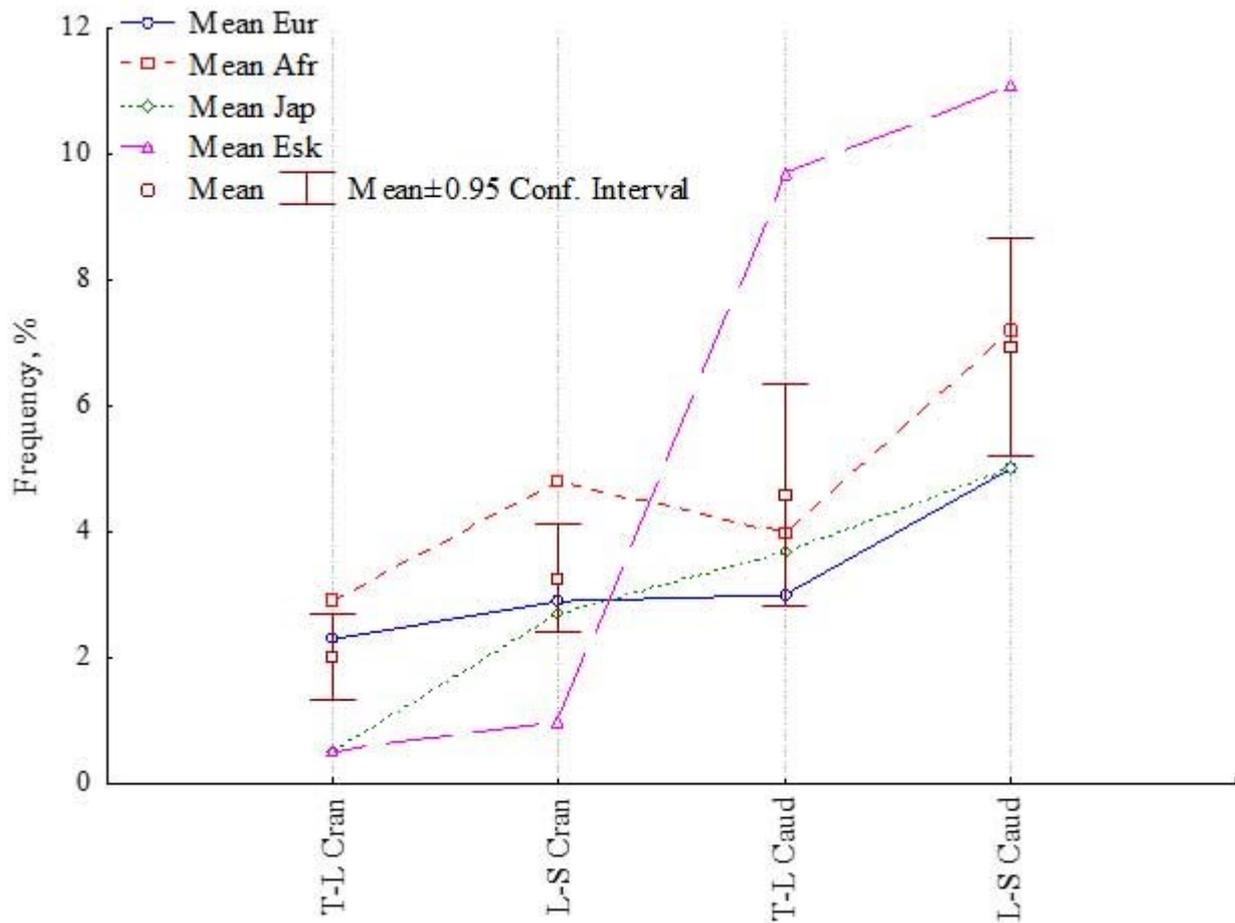| Sample	T9 inf. rib fac. on the body	T10 rib fac. at transverse pr.	T12 type of sup. art. proc.	L1 type of sup. art. proc.
Ekv	19.6	23.1	40.0	40.0
NA Eur	15.6	19.2	22.6	28.6
Rus	19.6	33.0	27.7	45.5
NA Afr	18.9	21.1	40.3	57.1
χ^2-test	NS	NS	NS	NS

Fig 3. Frequency distribution of cranial (Cran) and caudal (Caud) shifts at T-L and L-S borders in various human population groups as plotted against mean human. Eur – groups of European ancestry; Afr – groups of African ancestry; Jap – Japanese; Esk – Eskimo/Inuit groups (based on data from Appendix 1-4).

Interestingly, these two geographical groups show opposite tendencies in spine patterning: highest frequencies of cranial border shifts and lowest of caudal are in groups of African ancestry (Bornstein and Peterson, 1966; Merbs, 1974; de Beer Kaufman, 1974), while the opposite is true for the Eskimo/Inuit groups.

One hypothesis is that the tendency towards caudal border shifts in Eskimo groups may be associated with the tendency towards relative dimensional elongation of the corpus, as it is known for the Asian groups that they are relatively short-legged with longer torso (Bogin and Varela-Silva, 2010). If numerical elongation of the pre-sacral spine was associated with increase in trunk length, this could indicate that the Eskimo ancestors were selected for numerically longer spines as one of the means to increase the trunk length. However, several facts do not support this hypothesis. First, differences between individuals with numerically elongated spines and those with modal number of vertebrae are no more than tendencies, not reaching the level of statistical significance, likely due to an effect of compensation (Lanier, 1939; Tague, 2018). Second, although Eskimos have higher ratio of trunk to lower limb length if compared to groups adapted to equatorial climate (Holliday and Hilton, 2010), Eskimos are relatively long-legged compared to other Asian groups (e.g. Chukchi, Buryats etc.) (Klevtsova and Smirnova, 1974). Thus, this tendency to caudalwards shifts in spine pattern should be even more expressed in other population groups of Asia. Unfortunately, we do not have data on other autochthon groups from Siberia, and in the literature only data on Japanese are available. Japanese, however, have low level of variation for both cranial and caudal shifts. Given the relatively weak correlation between cranio-caudal shifts in pattern at various spine levels, the above hypothesis would not explain by itself why Eskimos have increased predisposition for caudal shifts at other spine levels apart of L-S border, including the increased frequencies of elongated thoracic spines and the very strong tendency towards caudal shift at T9 level.

This brings to an assumption that the strong predisposition of the Eskimo groups to caudal shifts in spine patterning is related not so much to the relative lengthening of the corpus, but to the specific form and size of the thorax. Eskimos as well as other Arctic groups (e.g. Chukchi) are distinguished by large size and barrel-shaped forms of the thorax, which is viewed as an adaptation to the extremely cold environment, with lower availability of the oxygen and with the need to retain more heat within the body (thus, lower ratio of body surface to body volume) (Klevtsova and Smirnova, 1974). Taking this into account, the fact that Eskimos are predisposed to the increase in number of ribs at thoraco-lumbar border (caudal shift) may be associated with large size of the thorax. Interestingly, the greatest difference between the Ekven Eskimo group compared to groups of European and African ancestry is in a trait related to the position of the 10th rib's costo-central articulation. In the Ekven sample (both males and females) predominates the variant that in other population groups is much more characteristic for males than females (though sex differences are still significant in the Ekven sample). It is also of note that this particular trait seems to vary little among non-Eskimo samples when analysis is performed within each sex; and it shows high values of symmetry compared to other analyzed traits. In a previous work (Karapetian, 2015), it was argued that the position of the costo-central articulation of the 10th rib is related to the orientation of this rib in the thoracic cage. And this may have some morphological significance given that the 10th rib is usually the last non-floating rib, and it shows highly significant sex differences. Thus, it should be tested on living individuals using methods of visualization (CT of MRI) if the position of the costo-central articulation (shared between T9 and T10 or articulated only with T10) is related to more horizontal or more oblique orientation of the 10th rib, and if this trait is associated with the form of the thoracic cage.

Possible impact of environmental factors on the pattern of cranio-caudal shifts in the Eskimo groups should be discussed as well. Potentially, external factors may trigger homeotic transformations along the axial skeleton during embryogenesis, which is often seen in experimental animals under the influence of xenobiotics or maternal stress (Chernoff and Rogers, 2004). Decreased body temperature and hypoxia are among factors reported to cause developmental anomalies in the axial skeleton in mice embryo (Murakami and Kameyama, 1963; Lecyk, 1965), and comparable regularities may exist for humans. One way to assess a presence of the increased exogenous stress during prenatal development is to assess the level of fluctuating asymmetry – an often used measure of developmental instability (Van Valen, 1962). As the bilaterally symmetric organisms are preprogrammed to symmetry, deviations from symmetric state are viewed as "the random disturbances of patterns" (Van Valen, 1962 p.137), failure of an organism to become absolutely symmetric via influence of epigenetic mechanisms. The specific mechanism for the asymmetry in spine patterning was discussed by Galis and coauthors (Galis et al., 2006). They argue that often unilateral presence of cervical ribs in their sample of deceased human fetuses and infants indicates diminished coordination between the left and right somites during development (Galis et al., 2006). Retinoic acid was proposed as one of the signaling molecules, coordinating left-right patterning in vertebrates, as deficient retinoic acid signaling induced bilateral asymmetry in experimental animal models (Vermot et al., 2005). Following Vermot and coauthors (Vermot et al., 2005), Galis and coauthors propose that deficient signaling may cause acceleration of somitogenesis on one side leading to differential left-right expression of *Hox* genes, controlling anterior-posterior patterning of the axial skeleton (Galis et al., 2006).

One way to assess if the Eskimo groups experience increased level of developmental instability, is to see if these samples show higher levels of homeotic transformations and higher level of asymmetry. The Eskimo samples, especially the Sadlermiut Inuit sample, indeed show on an average slightly higher frequencies of variations compared to the mean human values. However, higher frequencies are solely due to higher frequencies of the caudal border shifts, which may be an indicator of selective pressure favoring these variants, rather than increased level of developmental instability. Another argument would be that there are minimal cases of cervical ribs in the Eskimo/Inuit samples. While C-T border forms earlier in embryogenesis it is theoretically more vulnerable to the influence of factors, altering the development of the fetus, compared to T-L or L-S borders that form later in embryogenesis (see discussion in Galis et al., 2006). Thus if external factors are responsible for the pattern of variations in the vertebral columns of the Eskimo groups, C-T border should be more prone to variations compared to groups living in less stressful environmental conditions. Obviously, in the Eskimo samples there might be stronger prenatal/early postnatal selection against individuals with developmental abnormalities, associated with cervical ribs, due to greater constrains on the organism. When the Ekven sample was tested for differences in the levels of asymmetry in spine traits compared to studied samples of European and African ancestry, all samples showed approximately the same level of asymmetry without any statistically significant deviations.

Overall, the hypothesis that the Eskimo groups experienced higher level of instability in the axial skeleton development due to the influence of environmental factors is possible. However, the present data are more in agreement with inherent characteristics and existence of selective pressure favoring certain morphological variants. This should be tested by studying other groups adapted to living in the Arctic (primarily Chukchi) and compared to other Asian groups living in more southern areas.

CONCLUSION

Our study is consistent with increased predisposition of the temporally and geographically variable Eskimo/Inuit groups towards caudal shifts in spine patterning. This points to conservation of possibly adaptive traits that formed early in the history of this population.

REFERENCES

ALEXEEVA TI, BUZHILOVA AP, MEDNIKOVA MB, DOBROVOLSKAYA MV, editors (2008) Antropoekologiya severo-vostochnoy Azii: Chukota, Kamchatka, Komandorskiye ostrova. Taus, Moscow.

ALLBROOK DB (1955) The East African vertebral column: a study in racial variability. *Am J Phys Anthropol*, 13: 489-513.

ARUTYUNOV SA, SERGEEV DA (1975) *Problemy etnicheskoy istorii Beringomorya: Ekvenskiy mogilnik*. Direkt-Media, Moscow.

BOGIN B, VARELA-SILVA MI (2010) Leg length, body proportion, and health: a review with a note on beauty. *Int J Environ Res Public Health*, 7(3): 1047-1075.

BORNSTEIN PE, PETERSON RR (1966) Numerical variation of the presacral vertebral column in three population groups in North America. *Am J Phys Anthropol*, 25(2): 139-146.

BUIKSTRA JE, UBELAKER DH (1994) *Standards for Data Collecting from Human Skeletal Remains*. Arkansas Archaeological Survey, Fayetteville.

CHERNOFF N, ROGERS JM (2004) Supernumerary ribs in developmental toxicity bioassays and in human populations: incidence and biological significance. *J Toxicol Environ Health*, Part B, 7: 437-449.

DE BEER KAUFMAN P (1974) Variation in the number of presacral vertebrae in Bantu-speaking South African Negroes. *Am J Phys Anthropol*, 40: 369-374.

DZUPA V, SLEPANEK M, STRIZ M, KRBEC M, CHMELOVA J, KACHLIK D, BACA V (2014) Developmental malformations in the area of the lumbosacral transitional vertebrae and sacrum: differences in gender and left/right distribution. *Surg Radiol Anat*, 36(7): 689-693.

FRIESEN TM, MASON OK, editors (2016) The Oxford handbook of the Prehistoric Arctic. Oxford University Press, New York.

GALIS F, VAN DOOREN TJM, FEUTH JD, METZ JA, WITKAM A, RUINARD S, STEIGENGA MJ, WIJNAENDTS LC (2006) Extreme selection in humans against homeotic transformations of cervical vertebrae. *Evolution*, 60: 2643-2654.

GRAY H (1858) *Anatomy descriptive and surgical*. John W. Parker and Son, West strand, London.

HOLLIDAY TW, HILTON CE (2010) Body proportions of circumpolar peoples as evidenced from skeletal data: Ipiutak and Tigara (Point Hope) versus Kodiak Island Inuit. *Am J Phys Anthropol*, 142: 287-302.

JANKAUSKAS R (1988) Morphologicheskiye osobennosti pozvonochnogo stolba i factori ego izmenchivosti [PhD thesis]. Vilnius, Vilnius University.

KARAPETIAN MK (2015) Costal facet variations on the eighth, ninth and tenth thoracic vertebrae: association with sex and shifts in the cranio-caudal pattern of the human axial skeleton. *Eur J Anat*, 19(2): 179-188.

KLEVTSOVA NI, SMIRNOVA NS (1974) Morphologicheskiye osobennosti tela chukchey i eskimosov. *Voprosi antropologii*, 48: 18-33.

KÜHNE K (1932) Die Vererbung der variationen der menschlichen Wirbelsäule. *Z Morphol Anthropol*, Bd. 30(1/2): 1-221.

LANIER RR (1939) The presacral vertebrae of American White and Negro males. *Am J Phys Anthropol*, 25: 341-420.

LECYK M (1965) The effect of hypothermia applied in the given stages of pregnancy on the number and form of vertebrae in the offspring of white mice. *Experientia*, 21(8): 452-453.

MALLO M, WELLIK DM, DESCHAMPS J (2010) *Hox* genes and regional patterning of the vertebrate body plan. *Dev Biol*, 344: 7-15.

MERBS CF (1974) The effects of cranial and caudal shift in the vertebral columns of northern populations. *Arctic Anthropol*, 11: 12-19.

MERBS CF (2004) Sagittal clefting of the body and other vertebral developmental errors in Canadian Inuit skeletons. *Am J Phys Anthropol*, 123(3): 236-249.

MURAKAMI U, KAMEYAMA Y (1963) Vertebral malformations in the mouse foetus caused by maternal hypoxia during early stages of pregnancy. *J Embryol Exp Morph*, 11: 107-118.

NAKAJIMA A, USUI A, HOSOKAI Y, KAWASUMI Y, ABIKO K, FUNAYAMA M, SAITO H (2014) The prevalence of morphological changes in the thoracolumbar spine on whole-spine computed tomographic images. *Insights Imaging*, 5: 77-83.

RAGHAVAN M, DEGIORGIO M, ALBRECHTSEN A, MOLTKE I, SKOGLUND P, KORNELIUSSEN TS, GRØNNOW B, APPELT M, GULLØV HC, FRIESEN TM, FITZHUGH W, MALMSTRÖM H, RASMUSSEN S, OLSEN J, MELCHIOR L, FULLER BT, FAHRNI SF, STAFORD T, GRIMES V, RENOUF MAP, CYBULSKI J, LYNNERUP N, LAHR MM, BRITTON K, KNECHT R, ARNEBORG J, METSPALU M, CORNEJO OE, MALASPINAS AS, WANG Y, RASMUSSEN M, RAGHAVAN V, HANSEN TVO, KHUSNUTDINOVA E, PIERRE T, DNEPROVSKY K, ANDREASEN C, LANGE H, HAYES MG, COLTRAIN J, SPITSYN VA, GÖTHERSTRÖM A, ORLANDO L, KIVISILD T, VILLEMS R, CRAWFORD MH, NIELSEN FC, DISSING J, HEINEMEIER J, MELDGAARD M, BUSTAMANTE C, O'ROURKE DH, JAKOBSSON M, GILBERT MTP, NIELSEN R, WILLERSLEV E (2014) The genetic prehistory of the New World Arctic. *Science*, 345(6200): 1255832-1-9. doi: 10.1126/science.1255832

SCHAEFER M, BLACK S, SCHEUER L (2009) *Juvenile Osteology: a laboratory and field manual*. Academic Press, Burlington.

SCHAPERA J (1987) Autosomal dominant inheritance of cervical ribs. *Clin Genet*, 31: 386-388.

SCHULTZ AH (1930.) The skeleton of the trunk and limbs of higher primates. *Hum Biol*, 2: 303-438.

SCHUMACHER R, MAI A, GUTJAHR P (1992) Association of rib anomalies and malignancy in childhood. *Eur J Pediatr*, 151: 432-434.

SCHMORL G, JUNGHANNS H (1971) *The human spine in health and disease*. Grune & Stratton, New York.

SHORE LR (1930) Abnormalities of the vertebral column in a series of skeletons of Bantu natives of South Africa. *J Anat*, 64: 206-238.

SINGER KP, BREIDAHL PD (1990) Accessory ossification centres at thethoracolumbar junction. *Surg Radiol Anat*, 12: 53-58.

STATISTICA (data analysis software system) [Computer program]. Version 8.0. Tulsa (OK): StatSoft Inc., 2007.

STEWART TD (1932) The vertebral column of the Eskimo. *Am J Phys Anthropol*, 17: 123-136.

TAGUE RG (2018) Proximate cause, anatomical correlates, and obstetrical implication of a supernumerary lumbar vertebra in humans. *Am J Phys Anthropol*, 165 (3): 444-456.

TEN BROEK CMA, BAKKER AJ, VARELA-LASHERAS I, BUGIANI M, VAN DONGEN S, GALIS F (2012) Evo-devo of human vertebral column: on homeotic transformations, pathologies and prenatal selection. *Evol Biol*, 39: 456-471.

THOMPSON NE, ALMÉCIJA S (2017) The evolution of vertebral formulae in Hominoidea. *J Hum Evol*, 110: 18-36.

TODD TW (1922) Numerical significance in the thoracolumbar vertebrae of the mammalian. *Anat Rec*, 24: 261-286.

TROTTER M (1929) The vertebral column in Whites and in American Negroes. *Am J Phys Anthropol*, 13: 95-107.

TULSI RS (1972) Vertebral column of the Australian aborigine: selected morphological and metrical features. *Z Morphol Anthropol*, 64: 117-144.

VAN VALEN L (1962) A study of fluctuating asymmetry. *Evolution*, 16(2): 125-142.

VERMOT J, GALLEGO LLAMAS J, FRAULOB V, NIEDERREITHER K, CHAMBON P, DOLLÉ P (2005) Retinoic acid controls the bilateral symmetry of somite formation in the mouse embryo. *Science*, 308: 563-566.

WILLIAMS SA, MIDDLETON ER, VILLAMIL CI, SHATTUCK MR (2016) Vertebral numbers and human evolution. *Am J Phys Anthropol*, 159(Suppl 61): S19-36.

Appendix 1. Frequency distribution of spines with agenesis of the 12th pair of ribs (cranial shift at T-L border) in various human groups. Based on this study and literature sources.

Sample[a]	% with trait	Data source
Moscow	2.7	This study
Kozino, Moscow reg.	1.9	This study
Lithuania	3.5	Jankauskas, 1988
Europe	2.1	Schultz, 1930
USA Eur	0.7	This study
USA Eur	1.0	Borstein and Peterson, 1966
USA Eur (Males)	2.0	Lanier, 1939
Canada Eur	4.2	This study
USA Afr	3.0	This study
USA Afr	1.4	Borstein and Peterson, 1966
USA Afr	5.2	Trotter, 1929
USA Afr	4.7	Schultz, 1930
USA Afr (Males)	2.0	Lanier, 1939
S. Africa (Bantu)	3.7	Shore, 1930
East Africa	0.5	Allbrook, 1955
Australia (aborigines)	3.2	Tulsi, 1972
Japan	0.9	Nakajima et al., 2014
Japan	0.0	Hasebe, cited by: Schultz, 1930
Japan	1.0	Kubo, cited by: Schultz, 1930
Japan	0.0	Nishi, cited by: Schultz, 1930
N-W Coast Indians	5.1	Merbs, 1974
Mixed Native	0.4	Borstein and Peterson, 1966
Alaska North	0.0	Stewart, 1932
Alaska South	0.0	Stewart, 1932
Sadlermiut	1.4	Merbs, 1974
Ekven	0.0	This study
Mean Eur (SD)	2.3(1.2)	8 samples
Mean Afr (SD)	2.9(1.7)	7 samples
Mean Japan (SD)	0.5(0.6)	4 samples
Mean Eskimo (SD)	0.4(0.7)	4 samples
Mean human (95CI)	1.9(1.3-2.6)	26 samples

[a]Eur – European ancestry; Afr – African ancestry.

Appendix 2. Frequency distribution of spines with ribs at 20th vertebra level (13 thoracic, caudal shift at T-L border) in various human groups. Based on this study and literature sources.

Sample	% with trait	Data source
Moscow	1.3	This study
Kozino, Moscow reg.	0.0	This study
Lithuania	1.0	Jankauskas, 1988
Europe	3.9	Schultz, 1930
USA Eur	3.1	This study
USA Eur	9.8	Borstein and Peterson, 1966
USA Eur (Males)	10.0[a]	Lanier, 1939
Canada Eur	2.1	This study
USA Afr	0.0	This study
USA_Afr (Males)	12.0[a]	Lanier, 1939
USA Afr	7.4	Borstein, Peterson, 1966
USA Afr	2.1	Trotter, 1929
USA Afr	6.3	Schultz, 1930
East Africa	4.3	Allbrook, 1955
Australia	1.9	Singer and Breidahl, 1990
Australia (aborigines)	1.6	Tulsi, 1972
Japan	5.8	Nakajima et al., 2014
Japan	6.1	Hasebe, cited by Schultz, 1930
Japan	3.0	Kubo, cited by Schultz, 1930
Japan	0.0	Nishi, cited by Schultz, 1930
Mixed Native	3.8	Borstein and Peterson, 1966
N-W Coast Indians	12.8	Merbs, 1974
Sadlermiut	15.7	Merbs, 1974
Alaska North	10.3	Stewart, 1932
Alaska South	7.3	Stewart, 1932
Ekven	5.4	This study
Mean frequency Eur (SD)	3.0(3.3)	7 samples
Mean frequency Afr (SD)	4.0(3.0)	5 samples
Mean frequency Japan (SD)	3.7(2.8)	4 samples
Mean frequency Eskimo (SD)	9.7(4.5)	4 samples
Mean human (95CI)	4.8(3.0-6.5)	24 samples

[a]Here cases of vertebrae with facets on the pedicles also included, which does not represent a case of true ribs (see Mann, Hunt, 2005). "The percentages are not strictly comparable to those reported by Fischel, Rabl, Adolphi, Bardeen, Kubo, Hasebe, Schultz, and Stewart for the presence of thirteen thoracic vertebrae. This is due to the inclusion in the observations on American males the presence of facets for separate processes, often small enough to elude preservation unless caution to preserve them" (Lanier, 1939 p.410).

Appendix 3. Frequency distribution of spines with L5 sacralization (23 PCV) in various human groups. Based on this study and literature sources.

Sample	% with trait	Data source
Moscow	2.8	This study
Kozino, Moscow reg.	0.0	This study
Russia	5.0	Turner, cited by: Schmorl and Junghanns, 1971
Lithuania	1.5	Jankauskas, 1988
Norway	5.3	Ingebrigtsen, cited by: Schmorl and Junghanns, 1971
Germany	1.0	Lübke, cited by: Schmorl and Junghanns, 1971
Europe	2.8	Shultz, 1930
USA Eur	3.3	This study
USA Eur	4.3	Borstein and Peterson, 1966
USA Eur	2.7	Tague, 2018
Canada Eur	2.9	This study
Lapland (Saami)	0.7	Ingebrigtsen, cited by: Schmorl and Junghanns, 1971
Japan	2.7	Nakajima et al., 2014
Japan	2.8	Hasebe, cited by Schultz, 1930
Japan	2.7	Nishi, cited by Schultz, 1930
USA Afr	4.5	This study
USA Afr	7.4	Borstein and Peterson, 1966
USA Afr	4.7	Tague, 2017
USA Afr	10.3	Trotter, 1929
USA Afr	3.1	Schultz, 1930
USA Afr	1.3	Willis, cited by: Schultz, 1930
S. Africa (Bushman)	7.1	De Beer Kaufman, 1974
S. Africa (Bantu)	5.8	De Beer Kaufman, 1974
East Africa	3.4	Allbrook, 1955
S. Africa (Bantu)	0.0	Shore, 1930
Australia (aborigines)	4.8	Tulsi, 1972
N-W Coast Indians	2.6	Merbs, 1974
Mixed Native	3.0	Borstein, Peterson, 1966
Alaska North	0.0	Stewart, 1932
Alaska South	0.0	Stewart, 1932
Sadlermiut	2.9	Merbs, 1974
Ekven	0.0	This study
Mean Eur (SD)	2.9(1.6)	11 samples
Mean Afr (SD)	4.8(3.0)	10 samples
Mean Japan (SD)	2.7(0.06)	3 samples
Mean Eskimo (SD)	0.7(1.5)	4 samples
Mean human (95CI)	3.2(2.3-4.0)	32 samples

Appendix 3. Frequency distribution of spines with S1 lumbalization (25 PCV) in various human groups. Based on this study and literature sources.

Sample	% with trait	Data source
Moscow	4.4	This study
Kozino, Moscow reg.	2.8	This study
Germany	9.0	Lübke,cited by: Schmorl and Junghanns, 1971
Europe	4.9	Shultz, 1930
USA Eur	7.0	This study
USA Eur	5.3	Borstein and Peterson, 1966
USA Eur	6.7	Tague, 2018
Canada Eur	6.0	This study
Lithuania	3.0	Jankauskas, 1988
Czech Republic	0.4	Dzupa et al., 2014
Japan	6.2	Nakajima et al., 2014
Japan	2.6	Hasebe, cited by Schultz, 1930
Japan	6.1	Nishi, 1928, cited by Schultz, 1930
USA Afr	0.0	This study
USA Afr	3.1	Borstein and Peterson, 1966
USA Afr	6.2	Shultz, 1930
USA Afr	4.1	Willis, 1923, cited by: Schultz, 1930
USA Afr	8.2	Trotter, 1929
USA Afr	4.8	Tague, 2017
S. Africa (Bushman)	17.9	De Beer Kaufman, 1974
S. Africa (Bantu)	10.8	De Beer Kaufman, 1974
S. Africa (Bantu)	5.0	Shore, 1930
East Africa	11.7	Allbrook, 1955
Australia (aborigines)	4.0	Tulsi, 1972
N-W Coast Indians	19.2	Merbs, 1974
Mixed Native	8.5	Borsteit, Peterson, 1966
Alaska North	13.2	Stewart, 1932
Alaska South	10.7	Stewart, 1932
Saldermiut	8.6	Merbs, 1974
Ekven	12.8	This study
Mean Eur (SD)	5.0 (2.5)	10 samples
Mean Afr (SD)	7.2 (5.1)	10 samples
Mean Japan (SD)	5.0 (2.0)	3 samples
Mean Eskimo (SD)	11.3 (2.1)	4 samples
Mean human (95CI)	7.1(5.4-8.8)	30 samples