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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

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SUMMARY

Different variants of the ninth and tenth thoracic vertebrae are described in the literature with little information on their prevalence in human populations. To review this question, 5 osteological samples from different geographical areas were studied for the presence of costal facets on the eighth (T8), ninth (T9) and tenth (T10) thoracic vertebrae. We found that inferior costal facets on vertebral centrum were absent bilaterally in 1.5% of T8 and in 46% of T9; costal facets on both T10 transverse processes were absent in 39% of cases. Absence of inferior costal facets on the T8 and T9 centrum and costal facets on the T10 transverse processes was positively associated with cranial shifts at regional borders of the spine. However, additional analysis revealed that the position of the costo-central articulation at the level of T8 and T9 as well as the position of the most inferior "typical" thoracic vertebra significantly depended on sex (p<0.001). Sex differences were most pronounced at the level of T9 where females showed very frequent absence of inferior costal facets (76% of cases compared to 47% in males). This suggests a difference in an average 10th rib position in relation to the spine in females. Significant sex differences in the position of the most inferior "typical" thoracic vertebra may be partially explained by the fact that females in general are more likely to develop some forms of cranial shifts. However, according to the literature, the female axial skeleton possesses a complex of morphological features that is seen as an adaptation to pregnancy. In this view, the different position of the female 10th rib may be one component of the complex.

Key words: Axial skeleton – Homeotic shifts – Sexual dimorphism – 8th -10th thoracic vertebrae – Costo-central articulation – Costo-transverse articulation

INTRODUCTION

Nonmetric features of the human skeleton have attracted some attention due to their usefulness in studying population-based variability and genetic distances (Finnegan, 1978; Ossenberg, 1976; Buikstra and Ubelaker, 1994; Hanihara et al., 2003), as well as due to their clinical and medico-legal significance (e.g. Schumacher et al., 1992; Wight et al., 1999; Kanchan et al., 2009; Verna et al., 2013). One of such nonmetric features is a group of anatomical variations in the area of the eighth (T8), ninth (T9) and tenth (T10) thoracic vertebrae which, with few exceptions (Struthers, 1874; Lanier, 1939), were not previously subjected to detailed study.

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The “typical” thoracic vertebra has superior and inferior costal demi-facets on the centrum, and thus articulates with four ribs, sharing rib articulations with the vertebrae above and below. Additionally, this vertebra has costal facets on the transverse processes that articulate with the tubercles of the superior ribs (White and Folkens, 2005). The area of T8-T10 is a transitional zone from “typical” to special thoracic vertebrae which corresponds to a transition from true to false ribs (ribs 8-12). Unfortunately, there is some confusion in the literature concerning the morphology of this zone, specifically the 9th thoracic vertebra. For example, according to Gray (1858), T9 has only superior demi-facets and T10 has complete superior costal facets on the centrum. A similar description of these vertebrae is given by Saladin (2012). However, according to other sources, T9 is classified as a “typical” thoracic vertebra, which would mean that it has inferior costal demi-facets on the centrum (Prives et al., 1989; White and Folkens, 2005). The somehow contradicting data may indicate that T9 morphology might be subject to variation, and although most authors are consistent in describing T10, there are indications that the morphology of this vertebra also varies. Indeed, Struthers studied T9 and T10 vertebrae on a sample of 21 individuals, and concluded that costal facets cannot be used to reliably characterize these two vertebrae (Struthers, 1874). High variability of T10 costal facets was also observed by Lanier (1939).

It is known that vertebrae located at regional borders of the spine always have a “transitional” morphology, i.e. while having main characteristics of a region to which they belong, they also have some characteristics of the adjacent region (White and Folkens, 2005). According to Kühne (1932), similarity of vertebrae located on the border between two regions with those of the adjacent region can be of different degree through various morphological changes of vertebrae themselves and of corresponding costal elements. Vertebrae assuming more characteristics of the adjacent region than is usually observed mark a shift in the cranio-caudal pattern of the spine. In extreme cases when identity of a vertebra changes, for example when a cervical vertebra assumes thoracic morphology, this indicates a homeotic transformation along the axial skeleton (Galis et al., 2006). In Kühne’s definition, cranial shift (tendency) includes all cases where regional borders are completely or only partially shifted toward the cranium (*cranialwärts*). Caudal tendency shows opposite direction (*caudalwärts*) of complete or partial shift (Kühne, 1932).

Existence of genetic predisposition to homeotic shifts in spine pattern was confirmed by family studies (e.g. Kühne, 1932; Williams, 1965); however, possible impact of external factors is also suggested (e.g. Murakami and Kameyama, 1963; Chernoff and Rogers, 2004). According to Kühne (1932) only the direction of the shift is inherited, but not its exact manifestation. At present, it is known that anterior (cephalad) or posterior (caudad) homeotic transformations along the axial skeleton have something to do with altered expression of *HOX* genes during embryogenesis (Mallo et al., 2010).

It is quite logical to see variation in the position of the most inferior “typical” thoracic vertebra and the presence or absence of costal facets on the T10 transverse processes as minor manifestations of a tendency toward cranial or caudal shift in spine morphology. This supposition is in agreement with Lanier’s observation that capitular articulation of the 10th rib limited to the T10 centrum is most often seen in “cranial columns”, while the presence of costal facets on the transverse processes of T10 is seen more often in “caudal columns” compared to “cranial columns” (Lanier, 1939). Accordingly, the goal of the current study is to analyze frequency distributions of different T8-T10 variants, as well as to examine the association of costal facet variations with sex and with cranial or caudal shifts at cervico-thoracic (C-T), thoraco-lumbar (T-L) and lumbo-sacral (L-S) borders.

MATERIALS AND METHODS

The study was performed on five osteological samples totaling 480 individuals that included US residents of European and African descent (20th C., Terry collection, Smithsonian Institution), Canadian residents of predominantly European descent

Table 1. Main characteristics of the study samples

Collection	Origin	Abbreviation	Chronology	Sex	N
Terry collection (Whites), Smithsonian institution	Missouri, USA	AW – American Whites	1924-1966	♂	71
				♀	63
Terry collection (Blacks), Smithsonian institution	Missouri, USA	AB – American Blacks	1932-1966	♂	34
				♀	36
Grant collection, Toronto University	Toronto, Canada	CA – Canadian residents	1931-1950	♂	80
				♀	17
MSU Anthropology Department collection	Moscow city, Russia	RC – Russian residents (city)	1950th	♂	64
				♀	13
Kozino collection, Research Institute and Museum of Anthropology, MSU	Kozino village, Moscow region	RV – Russian residents (village)	18th C.	♂	64
				♀	38

(20th C., Grant collection, University of Toronto Department of Anthropology), Moscow city residents (20th C., anatomical collection of the Lomonosov Moscow State University [MSU] Department of Anthropology) and 18th century Russian peasants (Kozino collection, Research Institute and Museum of Anthropology, MSU). Detailed description of the material is given in Table 1.

The Terry and the Grant collections consist of individuals of known sex and age (Hunt and Albanese, 2005; Bedford et al., 1993). The collection of Moscow city residents represents skeletons from unclaimed bodies and in many respects is similar to that of the Terry and the Grant collections, except that age and sex were not documented prior to skeletonization. The collection of Russian peasants originates from a rural cemetery near Zvenigorod city (Moscow region) and represents individuals who lived and died in the village during the 18th century. For individuals from the two Russian collections, sex was estimated using morphological features on the pelvis, skull and the distal part of the humerus (Phenice, 1969; Acsádi and Nemeskéri, 1970; Rogers, 1999).

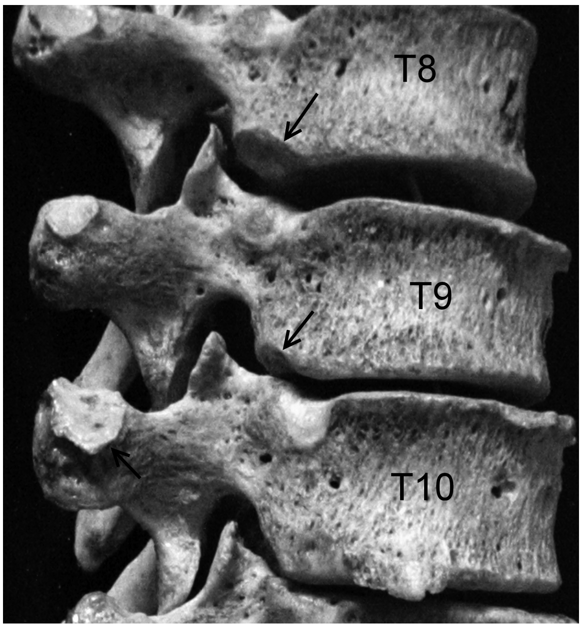
Sampling from the Terry collection was done on a random basis within sex, age (10 year intervals) and population groups (Whites and Blacks). The same sampling procedure was done for males from the Grant collection, while females from this collection were almost all included in the study. The two Russian samples represented all individuals from the collections that had completed or almost completed their growth. All individuals in the study were 18 years of age and older with no signs of severe pathologies and with complete or almost complete vertebral column.

Each spine was studied for a presence of inferior costal facets on T8 and T9 (the 15th and 16th vertebrae), and for a presence of costal facets on the transverse processes of T10 (the 17th vertebra) (Fig. 1). Unilateral and bilateral variants were recorded. A “standard” variant of T8 and T9 refers to the one with all 6 costal facets (2 superior and 2 inferior demi-facets on the centrum and two facets on the transverse processes). The last “typical” thoracic vertebra refers to the most inferior thoracic vertebra with both inferior costal demi-facets. A “standard” variant of T10 refers to the vertebra with costal facets on both transverse processes.

Presence of other developmental variations on the same pre-sacral spines was recorded, namely manifestations of cranial or caudal shift at regional borders of the spine.

Signs of cranial shift included:

- Cervical ribs. Their presence was scored when anterior (costal) parts of the transverse processes of C7 were not fused while there were articular facets on the centrum and on the posterior transverse processes.
- Tendency for cervical rib formation (rudimentary cervical ribs). This was scored if the anterior part of the C7 transverse process was present, but was enlarged beyond that of the posterior part, and/or there was a tendency toward separation of the costal element (Fig. 2).
- Lumbarization of T12 (no 12th ribs). Scored when both costal facets on the 19th vertebra



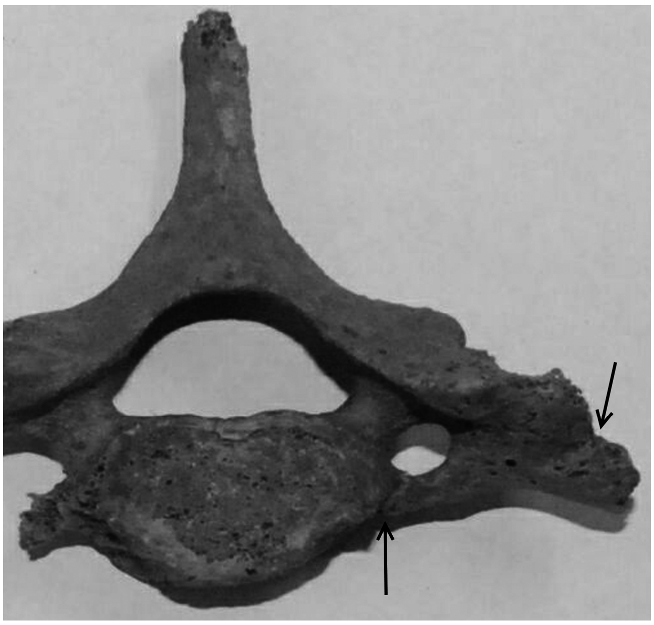


Fig. 1 (left). Inferior costal demi-facets on the T8 and T9 centrum and a costal facet on the T10 transverse process.

Fig. 2 (right). Rudimentary cervical rib. Note enlarged anterior part of the transverse process partially separated from the centrum (arrows).

were absent.

- T12 superior articular processes of the lumbar type. Scored after Lanier when the articular surfaces were “arcs of a circle whose center is posterior to the vertebral canal” (Lanier, 1939: p. 408), i.e. oriented dorso-medially.
- Partial sacralization of L5. Recognized by significantly enlarged transverse processes of the 24th vertebra sometimes articulating with the sacrum.
- Complete sacralization of L5 (23 presacral vertebrae). Recognized by its partial or complete fusion to the sacrum.

Signs of caudal shift

- Rudimentary lumbar ribs (separate transverse process). Scored when the transverse processes of the 20th vertebra were absent, rudimentary or there was an articular facet in the area of its attachment to the arch (Lanier, 1939; Mann and Hunt, 2005).
- Thoracalization of L1 (lumbar rib). Scored when a costal facet was seen on the centrum of the 20th vertebra (Mann and Hunt, 2005).
- L1 superior articular processes of the thoracic type. Scored after Lanier when the articular surfaces were “arcs of a circle the center of which lies anterior to the vertebral canal” (Lanier, 1939: p. 408), i.e. oriented dorso-laterally.
- Lumbarization of S1 (25 presacral vertebrae). Scored when S1 was completely separated from the sacrum.

Absence of the first pair of ribs at T1 level was not considered, as this variation was not encountered in the material.

The variations were recorded only for vertebrae with a certain numerical identity. Statistical analysis was performed in STATISTICA program (v. 8) (StatSoft, 2007) and Microsoft Excel (2006). Assessment of statistical significance was based on Pearson’s χ^2 test.

RESULTS

Overall, inferior costal facets were present bilaterally on 96.8% of T8 and on 43.8% of T9 vertebrae; T10 had costal facets on both transverse processes in only 46.5% of cases. Thus variants of T9 and T10 described as “standard” are seen in only about half of cases. Unilateral absence of inferior demi-facets on T8 was observed as frequently as bilateral (in 1.7 and 1.5% of cases respectively). However on T9 bilateral absence of inferior demi-facet was much more common than unilateral (46.0 vs. 10.2% of cases respectively), and the same can be said about costal facets on the transverse processes of T10 (39.4% bilateral and 14.1% unilateral absence).

When frequencies were calculated according to sex, there were significant sex differences in frequencies of different T8 and T9 variants (Table 2). Notably, absence of inferior costal facets on the T8 and T9 centrum was significantly more common in female groups (see Table 2). This is especially true of the 9th thoracic vertebra for which bilateral

Table 2. Group- and sex-specific frequencies of different T8 and T9 variants.

Inferior costal facet on the centrum	Frequencies (%)											
	Male samples					Female samples					All groups	
	AW	AB	CA	RC	RV	AW	AB	CA	RC	RV	♂	♀
8th thoracic vertebra												
Present bilat.	97.2	97.1	100.0	100.0	100.0	90.5	86.1	100.0	100.0	97.4	99.0	92.8
Absent	1.4	0.0	0.0	0.0	0.0	4.8	5.6	0.0	0.0	2.6	0.3	3.6
Absent unilat.	1.4	2.9	0.0	0.0	0.0	4.8	8.3	0.0	0.0	0.0	0.6	3.6
χ^2 (sex)											*14.1****	
9th thoracic vertebra												
Present bilat.	47.1	54.6	50.7	53.9	62.9	21.3	26.5	38.5	23.1	27.0	53.4	25.3
Absent	40.0	36.4	41.6	36.5	27.4	67.2	67.7	61.5	53.9	59.5	36.7	63.9
Absent unilat.	12.9	9.1	7.8	9.5	9.7	11.5	5.9	0.0	23.1	13.5	9.8	10.8
χ^2 (sample)	*4.8 (p=0.77)*					*6.1 (p=0.63)*						
χ^2 (sex)											*35.6****	

*** p < 0.001

Table 3. Group- and sex-specific frequencies of different T10 variants.

Costal facet on the transverse processes	Frequencies (%)											
	Males					Females					All groups	
	AW	AB	CA	RC	RV	AW	AB	CA	RC	RV	♂	♀
Present bilaterally	36.9	60.6	36.5	50.8	62.5	39.0	47.2	44.4	30.8	62.8	47.0	45.7
Absent	35.4	36.4	50.0	33.3	35.4	45.8	30.6	55.6	46.2	35.3	38.9	40.4
Absent unilaterally	27.7	3.0	13.5	15.9	2.1	15.3	22.2	0.0	23.1	2.9	14.1	13.9
χ^2 (sample)	*26.8****					*12.1 (p=0.14)*						
χ^2 (sex)											*0.1*	

absence is observed in 64% of females and in only 37% of males ($p<0.001$). As shown in Fig. 3, the last "typical" thoracic vertebra in the pooled male sample is most often T9 (54%). In the pooled female sample it is usually T8 (65%). Note that the variant where T7 is the last "typical" thoracic vertebra is almost absent in the male sample, but is present in about 8% of cases among females (see Fig. 3). It is noteworthy that inter-group variability in the position of the last "typical" thoracic vertebra and in frequencies of different T9 variants is non-significant ($p>0.05$), which indicates that observed sexual differences are systematic and not accidental.

For T10, on the contrary, inter-group variability of rib facets on the transverse processes was significant, but only for the male samples (Table 3). This variability, however, does not seem to depend on ancestry (European vs. African ancestry) and may be incidental. At the same time, when all samples were pooled according to sex, males and females

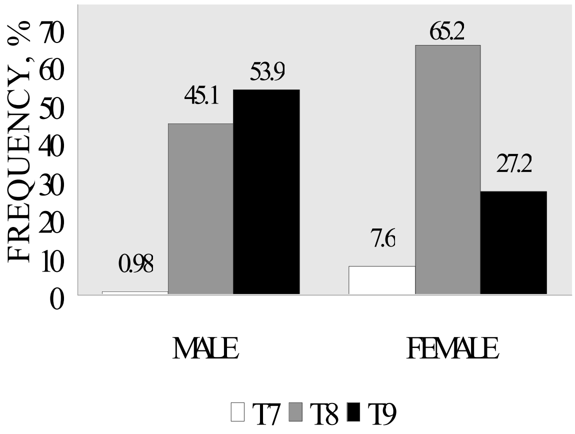


Fig. 3. Illustration of sex differences in the position of the most inferior thoracic vertebra having one or both inferior costal demi-facets (pooled data). *$\chi2$ (sex) = 38.8 ($p<0.001$).*

showed very similar frequencies of different T10 variants and sex differences were non-significant

Table 4. Frequency distribution of different anatomical variants of T9-T10 in male and female pooled samples, and test for association between presence of an inferior rib facet on the T9 centrum and a rib facet on the T10 transverse process. Left and right sides considered as separate observation.

Anatomical variant of T9-T10 segment	Frequency %		χ2 – test (sex)
	Males	Females	
1	**37.1**	20.1	26.0***
2	**20.4**	9.4	17.1***
3	16.8	**32.5**	27.6***
4	25.6	**37.9**	14.0***
χ2 – test (inferior rib facet on T9 centrum vs. rib facet on T10 transverse process)	33.1***	12.0***	-
N	558	298	-

*** p< 0.001. 1) 10th rib head articulates with the T9 and T10 centrum, rib facet on the T10 transverse process present; 2) 10th rib head articulates with the T9 and T10 centrum, no rib facet on the T10 transverse process; 3) 10th rib head articulates only with the T10 centrum, rib facet on the T10 transverse process present; 4) 10th rib head articulates only with the T10 centrum, no rib facet on the T10 transverse process.

Table 5. Association between costal facet variations on T8-T10 and cranial/caudal shifts at regional borders of the spine. Degree of correlation is expressed via posterior probability that one feature is present given the presence of another feature. Data pooled according to sex.

Feature A	Feature B	Females			Males		
		P(A|B)[1] (%)		χ2	P(A|B)	(%)	χ2
		Obs.	Exp.	(df=1)	Obs.	Exp.	(df=1)
No inferior costal facet on T8 centrum (bilateral or unilateral)	Cranial shift at C-T	11.8	7.1	3.0	5.6	1.0	3.9*
	Cranial shift at T-L	10.9	6.8	3.9*	0.0	1.0	1.1
	Cranial shift at L-S	16.7	7.2	2.0	0.0	1.1	0.2
	Caudal shift at T-L	0.0	6.8	0.8	0.0	0.9	0.5
	Caudal shift at L-S	16.7	7.0	1.1	0.0	1.1	0.1
No inferior costal facet on T9 centrum (bilateral or unilateral)	Cranial shift at C-T	87.5	75.0	1.5	77.8	47.3	7.1**
	Cranial shift at T-L	90.0	74.5	13.0***	61.9	46.7	15.3***
	Cranial shift at L-S	100.0	74.6	4.0*	65.0	49.0	2.1
	Caudal shift at T-L	66.7	74.4	0.1	30.8	46.7	1.2
	Caudal shift at L-S	33.3	74.7	4.8*	27.3	49.1	2.0
No costal facet on T10 transverse processes (bilateral or unilateral)	Cranial shift at C-T	73.3	54.2	2.2	64.7	54.2	0.8
	Cranial shift at T-L	67.2	54.1	8.0**	60.4	53.1	3.4
	Cranial shift at L-S	100.0	55.0	10.5**	63.2	53.7	0.8
	Caudal shift at T-L	45.0	53.9	0.0	47.4	52.9	0.0
	Caudal shift at L-S	40.0	54.0	0.2	54.5	53.6	0.2

[1]P(A|B) – posterior probability that trait A will occur given that trait B is present. Obs. – observed; Exp. – expected. χ2 – test for association with cranial/caudal shift, * p < 0.05; ** p < 0.01; *** p < 0.001

(see Table 3).

A Chi-square test showed that the presence of an inferior rib facet on the T9 centrum is significantly associated with the presence of a rib facet on the T10 transverse process (Table 4). However, this association is not strict, i.e. the two traits can appear independent of each other. Accordingly, four anatomical variants of T9-T10 region were identified (see Table 4) and these variants should represent different modes of the 10th rib attachment to the spine: 1 – 10th rib head articulates with the T9 and T10 centrum, rib facet on the T10 transverse process present (Fig. 1); 2 – 10th rib head articulates with the T9 and T10 centrum, no rib facet on the T10 transverse process; 3 – 10th rib head articulates only with the T10 centrum, rib facet on the T10 transverse process present; 4 – 10th rib head articulates only with the T10 centrum, no rib facet on the T10 transverse process. Frequency distributions of the four variants differ significantly between sexes (see Table 4). Namely, the first and second variants are significantly more common among males and the third and fourth variants are significantly more common among females. The main factor of this variability is significant sex difference in presence/absence of an inferior rib facet on the T9 centrum.

As expected, absence of rib facets on T8-T10 shows some tendency toward positive association with cranial shifts at regional borders of the spine. This association seems to be stronger in the pooled female compared to the pooled male sample (Table 5). And the strongest association seems to be between a cranial shift at the T-L border and absence of an inferior rib facet on the T9 centrum ($p<0.001$), observed in both male and female samples.

Although in females T10 rib facet variations are significantly associated with cranial shifts at T-L and L-S borders ($p<0.01$), in males this association does not reach the level of statistical significance (though tendencies exist, see Table 5).

DISCUSSION

In general, this study indicates that the costal facet morphology of T9 and T10 is quite variable, which supports Struthers' (1874) conclusion and corresponds to Lanier's (1939) data. At the same time, T8 morphology is relatively stable. All this information will be useful for correct identification of T8-T10 vertebrae in fragmented osteological material or on X-ray images. Obviously, use of "standard" criteria to identify these vertebrae by number may lead to false results, so their descriptions should be revised and sex-specific and population- specific frequencies of their different variants should be considered.

Recent studies revealed an existence of sex differences in axial skeleton morphology, which might be connected to the female's adaptation to her specific biological role (Bellemare et al., 2003; Bellemare et al., 2006; Mashrawi et al., 2010; Bastir et al., 2014). For example, Mashrawi et al. (2010) showed that inferior thoracic and superior lumbar vertebrae are significantly less kyphotic in females compared to males, female lumbar spinous processes are significantly thinner relative to the vertebral body height and in females T9, T10 and L1-L4 superior interfacet distances are wider relative to the vertebral body width. According to the authors, these features suggest "deeper lordosis-less kyphotic" spines in females (Mashrawi et al., 2010, p. 770). Bellemare et al. (2003; 2006) observed that females have different rib cage configuration compared to that of males. In particular, females' ribs have greater cranio-caudal inclination, greater length in relation to the stature and female's rib cage has smaller cross-section in relation to the diaphragm dome height below the T1. These differences may participate in forming a larger volume capacity of the rib cage relative to the size of the lung and a stronger contribution of an inspiratory rib muscles to the process of respiration in females, which according to the authors is an adaptation to a large abdominal distension due to pregnancy (Bellemare et al., 2003). On the other hand, Bastir et al. (2014) showed that in males compared to females the transverse processes of the thoracic vertebra are oriented more dorsally and cranially and the rib facets on them are also oriented more cranially. This may reflect a deeper placement of the vertebral column within the rib cage in males compared to females (Bastir et al., 2014). Also, everything else being constant, this would suggest that females' ribs in fact are oriented more horizontally than males'. Bastir et al. (2014) suggest that the greater rib inclination in females, observed by Bellemare et al. (2003), may be due to sex differences in rib curvature or in different position of the ribs within the costo-vertebral joints.

The current study's data suggest that the female 10th rib is placed somewhat differently in relation to the spine compared to that of the male. Namely, in females the capitular articulation is usually limited to the T10 centrum, while in males this articulation is most often placed more cranially and is shared between T9 and T10 centra. This doesn't seem to be a chance variation because of quite substantial sex differences in frequencies of the two variants ($p<0.001$). Interestingly, the 10th rib is the most inferior non-floating rib which also forms a part of an abdominal wall. Thus, the 10th rib position in relation to the 9th and 10th thoracic vertebrae might be an element of the above-described sexual dimorphism in axial skeleton morphology possibly related to the female's adaptation to pregnancy. To address this assumption, however, it is necessary to study the 10th rib itself and the association of its morphology or the position in the thoracic cage with the rib facet variations on the 9th and 10th thoracic vertebrae. Bastir et al. (2014) in the beginning of their study hypothesized that greater rib inclination in females, observed by Bellemare et al. (2003), may be due to higher position of the costo-transverse articulation relative to the corresponding costo-central articulation. And although their results do not support the hypothesis, the current study's data suggest that this might be the case for the 10th rib.

Interestingly, costal facet variations on the T9 centrum on one hand and the T10 transverse processes on the other are significantly associated, however costal facet variations on the T10 transverse processes do not show any stable pattern of sexual differences. Sexual dimorphism mainly concerns the position of the costo-central articulation and does not appear to influence the costo-transverse articulation. In this regard, it is necessary to know to what extent the T10 transverse process morphology is influenced by variation in morphology of the rib tubercle. For example, Struthers observed that absence of costal facets on the transverse processes of T10 was sometimes associated with absence of the tubercle on the 10th rib, but in other cases that the tubercle was moderately developed (Struthers, 1874). There is data that the 10th rib may be floating in some population groups (Saladin, 2012). In this regard it is interesting to know if absence of the rib facet on the T10 transverse process is associated and to what extent with a floating 10th rib.

On the other hand the current results suggest that variations of T8-T10 costal facets are not independent of other variations of the spine. Absence of costal facets on the inferior part of the T8 and T9 centrum and on the transverse processes of T10, showing tendencies toward association with "cranial phenotypes", may mark a developmental tendency toward homeotic shift in the vertebral pattern. This may represent posteriorization of T8, T9 and T10 identity, i.e. T8 and T9 assume the morphology of T10 and T10 that of T11 (by analogy with posteriorization of C7 identity, assuming thoracic morphology [Galis et al., 2006]). Thus, although relevant osteological and anthropological literature was mainly concerned with variations in the number of presacral or precaudal vertebrae and shifts at regional borders of the spine (e.g. Todd, 1922; Trotter, 1929; Schultz, 1939; Borstein and Peterson, 1966; Merbs, 1974; de Beer Kaufman, 1974, 1977), it is plausible that cranial or caudal tendencies can manifest themselves within a given region at an area of transitional morphology. Nevertheless, it is likely that T8 -T10 rib facet variations cannot be viewed completely as a manifestation of cranial shift. First, because frequencies of cranial/caudal shifts at the regional borders of the spine are far less frequent: e.g. 0-5% for presence of cervical ribs and absence of 12th ribs; 0.5-29% for lumbar ribs; 0-8% for cranial and 2-19.2% for caudal shift at L-S border (data from Trotter, 1929; Schultz, 1930; Shore 1930; Stewart, 1932; Lanier, 1939; Allbrook, 1955; Osburn, 1956; Borstein and Peterson, 1966; Tulsi, 1972; De Beer Kaufman, 1974; Merbs, 1974; Singer and Breidahl, 1990; Schumacher et al., 1992; Galis et al., 2006; Nakajima et al., 2014). Second, the associations between rib facet variation on the T10 transverse processes and shift at C-T, T-L and L-S borders are not significant for the male sample.

In females, relatively frequent absence of inferior rib facets at the level of T8 and T9 could be partially explained in view of association of these features with cranial shifts at regional borders of the spine. Indeed, many researchers point out that within a population females are more likely to have 23 presacral vertebrae, while columns with 25 presacral vertebrae are more often seen in males (e.g. Bornstein and Peterson, 1966; Merbs, 1974; De Beer Kaufman, 1974); also, cranial shifts at C-T and T-L borders are found somewhat more often in adult females compared to males (see Bornstein and Peterson, 1966: Table 2; Tulsi, 1972). It may be that females, who are on average shorter than males and thus have shorter trunks, are more likely to develop the "cranial phenotype" as a tendency toward shortening of the spine; and the opposite can be assumed about the "caudal phenotype". Indeed, it was shown that, in a male sample, individuals with shorter stature were more predisposed to cranial shifts compared to individuals of mean stature (Bardeen, 1900). Also, spines with cranial shifts were shown to be somewhat shorter on average and those with caudal shifts were longer than the spines with no signs of both (Lanier, 1939). It is also noteworthy that the highest frequencies of spines with 23 presacral vertebrae are observed in females of African ancestry (see Bornstein and Peterson, 1966: Table 4; Merbs, 1974: Table 2; De Beer Kaufman, 1974: Table 2) whose trunks are usually shorter compared to females of European and Asian ancestry of the same stature (Hrdličhka, 1928; Jason and Taylor, 1995). On the other hand, frequencies of homeotic shifts in the axial skeleton did not depend on sex in a sample of deceased fetuses and infants (Galis et al., 2006; ten Broek et al., 2012), so the question of sexual differences in frequencies of homeotic shifts needs further investigation.

Changes in the number of pre-sacral vertebrae or shifts at regional borders of the spine have long been classified as "variations" in contrast to developmental "malformations" (anomalies) (Schmorl and Junghanns, 1971). However, more recent data suggest that homeotic shifts along the axial skeleton may be a form of developmental anomaly, reflecting errors of morphogenesis, and may be associated with congenital malformations of other organ systems (Galis et al., 2006; ten Broek et al, 2012). According to experimental data, xenobiotics and/or maternal stress may cause development of supernumerary ribs in rodents (Chernoff and Rogers, 2004). And homeotic shifts may be caused in laboratory animals by mutations in different *Hox* genes (Mallo et al., 2010). The area of C-T junction seems to be one of the most critical, as a significant prenatal selection (spontaneous abortions) against individuals with cervical ribs was observed (Galis et al., 2006; ten Broek et al., 2012); and these individuals have increased susceptibility to develop a malignancy in early postnatal period (Schumacher et al., 1992; Zierhut et al., 2011). According to ten Broek et al. (2012), this is because of high interactivity between axial skeleton patterning and other morphogenetic processes at early organogenesis when C-T boundary is determined, as well as low redundancy of morphogens at this stage. At the same time, prenatal and early postnatal selection against homeotic shifts at T-L and L-S borders without shifts at C-T border seems to be much weaker (Galis et al., 2006; ten Broek et al., 2012).

Potential negative effects associated with homeotic transformations in general as well as possible existence of stabilizing selection could explain why some cranial or caudal shifts are quite rare in human adult populations. However, as regards the costal facet variations on T9 and T10, their frequent appearance may indicate that developmental processes, bringing these minor variations without accompanying changes at C-T border, are likely neutral and thus may be normal anatomical variations. On the other hand, presence of consistent and highly significant sexual differences at the level of T9 may indicate a functional significance of the described trait and possible directional selection acting on a female axial skeleton in the past. Also, it remains plausible that asymmetrical distribution of costal facets on T9 and T10, which is seen in only about 10-14% of cases, as well as asymmetrical T8 variants, may be somehow unfavorable, because this may represent slight asymmetry of somite development and rib position/ morphology.

Nonmetric variations of the spine have been used by some researchers for inter- group comparisons (Stewart, 1932; Lanier, 1939; Allbrook, 1955; Merbs, 1974; De Beer Kaufman, 1974, 1977) or as evidence of kinship and for personal identification purposes (Martin, Seller, 1958; Kanchan et al., 2009). As for the costal facet variations described in this article, their usefulness in inter-group comparisons needs to be studied in more detail, because these results do not show presence of consistent geographical differences in frequencies of these traits. For instance, the proportion of different morphological variants of T9 seems to be relatively stable in different populations when they are analyzed separately for each sex. And these data were not enough to discern any consistent pattern of T10 costal facet inter-group variability. However, variations of T8-T9 costal facets might be helpful in bioarchaeology as a supplementary data for sex estimation. Specifically, an individual with the last "typical" thoracic vertebra located on the level of T7–T8 is more likely to be a female than a male. And this should apply to subadults as well as to adults.

Overall, previously described "standard" variants of the ninth and tenth thoracic vertebrae were seen in only about half of all cases, while even the eighth thoracic vertebra in rare cases did not have "typical" morphology. The position of the last "typical" thoracic vertebra as well as different T8 and T9 variants significantly depend on sex. Inferior costal facets on T9 show the most pronounced sex differences. This suggests somewhat different 10th rib position in the female ribcage compared to that of the male. This study's data support the assumption that absence of inferior costal facets on the T8 and T9 centrum and costal facets on the T10 transverse processes are associated with cranial shifts in cranio-caudal pattern of the spine, though for males this association is not significant for rib facets on the T10 transverse processes. It seems that costal facet variations at the area of T8 -T10 have multifactorial origins.

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