A peer-reviewed version of this preprint was published in PeerJ on 17 April 2019.

View the peer-reviewed version (peerj.com/articles/6598), which is the preferred citable publication unless you specifically need to cite this preprint.

The coast of giants: An anthropometric survey of high schoolers on the Adriatic coast of Croatia

Pavel Grasgruber1*, Stipan Prce2, Nikola Stračárová1, Eduard Hrazdíra1, Jan Cacek1, Stevo Popović3, Sylva Hřebíčková1, Predrag Potpara3, Ivan Davidović4

1Faculty of Sports Studies, Masaryk University, Kamenice 5, 625 00 Brno, Czech Republic
2Gimnazija Metković, Ul. kralja Zvonimira 10, 20350, Metković, Croatia
3Faculty for Sport and Physical Education, University of Montenegro, Narodne omladine bb, 81400 Nikšić, Montenegro
4Ekonomska škola, Ul. Vladimira Rolovica 2, Bar, Montenegro

*Corresponding author: Pavel Grasgruber
E-mail: 32487@mail.muni.cz
Phone number: +420 608 569 374

ABSTRACT
The aim of this anthropometric survey was to map regional differences in height and body proportions in eight counties adjacent to the Adriatic coast of Croatia. Body height was measured in 1803 males and 782 females aged 17-20 years at 66 schools in 23 towns. When corrected for population size, average male height in the eight counties is 182.6 cm (182.8 cm in seven counties of Adriatic Croatia and 183.7 cm in four counties of Dalmatia proper). Regional variation is considerable (3.5 cm): from 180.6 cm in the county of Karlovac to 184.1 cm in the county of Split-Dalmacija. The height of females in the eight counties is 168.2 cm (168.3 cm in Adriatic Croatia and 168.5 cm in Dalmatia proper), but it is based on more limited data. The results show that young men from Dalmatia are currently the tallest in the world in the age category of 18 years, and the north-to-south gradient of increasing stature on the Adriatic coast largely mirrors that in Bosnia and Herzegovina (BiH). These parallel changes of height in Croatia and BiH can most likely be explained by unique genetic predispositions that are shared by the local populations of the Dinaric Alps.

Keywords: Croatia; Dalmatia; Dinaric Alps; height; body proportions
INTRODUCTION
Our previous study dealing with the stature of young males in Bosnia and Herzegovina (BiH) (Grasgruber et al., 2017) confirmed older reports according to which the people from the Dinaric Alps are one of the tallest in the world. It is obvious that they cannot currently reach their genetic potential due to poverty and a relatively poor quality of their diet, but given the presence of these factors, their height is even more remarkable. The height of young men from Herzegovina aged 17-20 years is 183.4 cm, which is only a slightly lower value than in the wealthy and well-fed Dutch (183.8 cm), who are officially the tallest in the world (Schönbeck et al., 2012). Furthermore, our comparisons indicate that local Muslim (Bosniak) men in Herzegovina are 2-3 cm shorter than Croats and Serbs living in the same regions or even the same towns. These differences in height are very strongly associated with the regional production of pork. Because pork is absent in the diet of Muslims for religious reasons, this result independently confirms the key role of high-quality nutrients from pork in child nutrition, as can be seen from our previous ecological studies (Grasgruber et al., 2014; Grasgruber et al., 2016).

The study of Pineau et al. (2005) performed between 2001-2003 showed that areas with extraordinary height are not limited to Herzegovina and have an analogy on the Adriatic coast in Dalmatia. This study covered the region of Split and Šibenik, Drniš, Sinj, Imotski, Vrgorac and Dubrovnik, but not northern Dalmatia (counties of Zadar and Lika-Senj) and the northern Adriatic coast of Croatia. The authors reported a mean height of 183.8 cm (n = 1253) in local males aged 17 years (J.-C. Pineau – pers. communication, 2013). The averages of high schools in individual towns ranged from 183.1 cm in Dubrovnik (n=259) through 184.5 cm in Split (n=875) to 187.0 cm in Drniš (n=21). These values are similar to those that we documented in Herzegovina. However, the pooled average of 18-to-19-year old boys in the Croatian capital of Zagreb was only 180.1 cm in 2010 (n=133) (Petranović et al., 2014). In a nationwide study performed between 2006-2008, the average height of Croatian boys aged 18 years was 180.5 cm (n=358) (Jureša et al., 2012).

These data strongly suggest that the Dalmatian phenomenon is only a regional anomaly and height decreases rapidly in the northern direction towards mainland Croatia. Indeed, historical data show that the average Croatian recruit around 1883 was 165.5 cm tall (Komlos, 2007), but height on the Adriatic coast ranged from 166 cm in Istria to 171 cm in southernmost Dalmatia (Coon, 1939). A large nationwide survey of school children performed in Croatia
between 1980-1984 in 36 towns/areas showed that these differences had persisted even after 100 years (Prebeg, 1988). At the age of 18 years, the height in some coastal and mainland regions differed by 4-5 cm. The shortest high schoolers came from the region of Zagorje north of Zagreb. To our knowledge, no later anthropometric survey used sufficiently representative samples of young males and females from the whole territory of Croatia. Therefore, mapping these geographical differences constitutes an intriguing challenge and the Adriatic coast is a particularly interesting territory in this regard.

Geographically, Adriatic Croatia is divided into two halves, which are separated by the mountain ranges of Velebit and Kapela. These mountains are a continuation of the main ridge of the Dinaric Alps in BiH and run through the rocky and sparsely inhabited county of Lika-Senj. They also separate the whole Adriatic coast from mainland Croatia. The region south of this mountain range is traditionally considered as ‘Dalmatia proper’ and consists of four counties (Zadar, Šibenik-Knin, Split-Dalmacija and Dubrovnik-Neretva), which include 0.86 million people (20% of the total Croatian population) (Croatian Bureau of Statistics, 2013a).

Although Dalmatia has a very pleasant Mediterranean climate, it has suffered from severe deforestation since the Neolithic (Kranjc, 2009), which led to the creation of an inhospitable ‘limestone desert’ covered by grass and bush. The local population has historically relied on pastoralism and at present, the inland Dalmatia is characterized by high rates of emigration for economic reasons. Furthermore, during the war events 1991-1995, ethnic tensions in the counties of Šibenik-Knin, Zadar, Lika-Senj and Karlovac led to the displacement of the local Serbian population. After the end of the war, the areas experienced an influx of Croatian (Catholic) refugees from BiH.

Because of these ongoing population changes, our research is one of the last opportunities to capture the original distribution of anthropological characteristics in this region. We were particularly interested in whether the north-to-south height gradient follows that documented in BiH – from 180.0 cm in Canton Una-Sana to 184.5 cm in the region of Trebinje. Therefore, we decided to include the whole area of coastal Croatia adjacent to the border of BiH.

METHODS
The research on the Adriatic coast of Croatia is a part of a larger anthropological project started in collaboration with the University of Montenegro in 2015. The aim of this project is
to provide detailed mapping of body height and some other anthropological characteristics on
the territory of the Dinaric Alps, which would enable better understanding of this intriguing
phenomenon. At present, this project already covers Bosnia, Herzegovina, Croatia, Montenegro and Kosovo. In addition, preliminary measurements of university students were
performed in Albania during the year 2017. The survey in Montenegro will be repeated in
2018.

The present study was realized within the project "Anthropological research of sports
potential in Dalmatia", number MUNI/A/1090/2016, with the support of the Specific
University Research Grant, as provided by the Ministry of Education, Youth and Sports of the
Czech Republic in the year 2016. Its primary objective was to measure body height and some
body proportions (sitting height, arm span) on the territory of Adriatic Croatia, as defined by
the Croatian Bureau of Statistics (Narodne novine, 2012). This region consists of seven
counties (županijas): Istra, Primorje-Gorski Kotar, Lika-Senj, Zadar, Šibenik-Knin, Split-
Dalmacija a Dubrovnik-Neretva. Total population in these seven counties is 1.41 million
(33% of the total Croatian population) (Croatian Bureau of Statistics, 2013). Because the
counties of Primorje-Gorski Kotar and Lika-Senj are largely separated by the mainland
county of Karlovac, we also decided to include the latter to have a more complete picture
(Fig. 1). The eight counties together comprise 1.54 million people (36% of the total Croatian
population).

**Target population.** The target population consisted of high schoolers (3rd and 4th graders)
aged 17-20 years. Similar to our previous study in BiH, we always tried to measure the
broadest spectrum of schools, from vocational to elite high schools (gimnazija). Our general
goal was to incorporate sufficiently representative samples of ≥ 200 individuals from each
region. For organizational or time reasons, it was not always possible to measure a
sufficiently large sample of both sexes and hence we again concentrated mainly on males. The
same limitations influenced the measurement of body proportions.

**Data collection.** The research was performed between April 2015-May 2017. Very few of the
schools contacted refused to participate, which allowed us to meet most of our goals. The
measurements were conducted using two devices – a mobile stadiometer SECA 213 and a
specially constructed apparatus designed for the measurement of height, sitting height and
arm span. The mutual compatibility and accuracy of these devices was tested on a sample of
91 Czech high schoolers. The mean difference in the measured height was only 1.5 mm (180.10 vs 180.25 cm).

Before the measurements, the students completed a short questionnaire, which included an informed consent agreement and questions about date of birth, place of residence and the level of education of the students’ parents. The results obtained during the survey were subsequently analyzed using the software Statistica 12. The values of height for each sample included means, standard deviations, medians, a range of extreme values, skewness, kurtosis and tests of normal distribution (Kolmogorov-Smirnov, Lilliefors and Shapiro-Wilk).

Figure 1 Political division of Croatia (counties/županije) with localities in which the measurements took place. Targeted counties are highlighted in green.
RESULTS

The research included measurements of body height in 1827 males and 792 females at 66 high schools in 23 towns (Fig. 1). Results of the individual schools are presented in Supplemental Table S1. Out of this sample, 1803 males and 782 females were incorporated into this study, because they listed a place of residence in the targeted eight counties (Supplemental Dataset, Sheets 1-2). Their age ranged between 17.1-20.8 years with a mean of 18.5 years in males and 18.6 years in females. The males were born between 1995-2000, the females between 1996-2000. The excluded males and females (n=34) came mostly from other Croatian counties, particularly from Sisak-Moslavina (n=9) and Zagreb (n=7), but some resided in BiH (n=11) (see Supplemental Dataset, Sheets 1-4).

Figure 2 Regional averages of male height on the Adriatic coast of Croatia and in Bosnia and Herzegovina (according to the self-reported place of residence), including average male height in individual towns (Table 3).
Male height. The average height of 1803 males residing in the eight examined counties was 182.7±6.7 cm. This mean did not change much, when only boys aged ≥18 years were considered (182.6±6.7 cm, n=1558), or when it was corrected for population size in these eight counties (182.6 cm) (Supplemental Table S2). After this correction, the average height is 182.8 cm in the seven counties of Adriatic Croatia and 183.7 cm in the four counties of Dalmatia proper. Regional differences were large (3.5 cm), from 180.6 cm in the county of Karlovac to 184.1 cm in the county of Split-Dalmacija (Table 1). All samples have a normal distribution of values (Table 2).

Table 1 Average male height in individual counties (županije) according to the self-reported place of residence.

<table>
<thead>
<tr>
<th>County (županija)</th>
<th>n</th>
<th>Average height (SD)</th>
<th>Range</th>
<th>Height (cm)</th>
<th>Range</th>
<th>Median</th>
<th>Above 190cm (%)</th>
<th>Above 200 cm (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Age (years)</td>
<td></td>
<td>Age (years)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Average (SD)</td>
<td>Average (SD)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Split-Dalmacija</td>
<td>438</td>
<td>18.3±0.4</td>
<td>17.5-19.8</td>
<td>184.1±6.9</td>
<td>165.0-204.5</td>
<td>183.9</td>
<td>79 (18.0%)</td>
<td>10 (2.3%)</td>
</tr>
<tr>
<td>Dubrovnik-Neretva</td>
<td>241</td>
<td>18.4±0.4</td>
<td>17.5-20.1</td>
<td>183.6±8.7</td>
<td>166.5-201.8</td>
<td>183.3</td>
<td>40 (16.6%)</td>
<td>2 (0.8%)</td>
</tr>
<tr>
<td>Šibenik-Knin</td>
<td>209</td>
<td>18.5±0.4</td>
<td>17.2-19.7</td>
<td>183.4±6.6</td>
<td>163.5-205.5</td>
<td>183.8</td>
<td>26 (12.4%)</td>
<td>2 (1.0%)</td>
</tr>
<tr>
<td>Zadar</td>
<td>249</td>
<td>18.4±0.4</td>
<td>17.3-20.2</td>
<td>182.8±6.2</td>
<td>167.1-200.7</td>
<td>182.8</td>
<td>31 (12.4%)</td>
<td>1 (0.4%)</td>
</tr>
<tr>
<td>Primorje-Gorski Kotar</td>
<td>238</td>
<td>18.7±0.4</td>
<td>17.6-20.4</td>
<td>181.9±6.7</td>
<td>163.0-198.5</td>
<td>181.8</td>
<td>29 (12.2%)</td>
<td></td>
</tr>
<tr>
<td>Istra</td>
<td>143</td>
<td>18.6±0.4</td>
<td>17.2-20.7</td>
<td>181.1±6.7</td>
<td>166.4-203.5</td>
<td>180.7</td>
<td>15 (10.5%)</td>
<td>1 (0.7%)</td>
</tr>
<tr>
<td>Lika-Senj</td>
<td>86</td>
<td>18.6±0.4</td>
<td>17.5-20.2</td>
<td>181.0±6.8</td>
<td>165.5-196.7</td>
<td>181.2</td>
<td>8 (9.3%)</td>
<td></td>
</tr>
<tr>
<td>Karlovac</td>
<td>199</td>
<td>18.7±0.5</td>
<td>17.2-20.5</td>
<td>180.6±6.2</td>
<td>162.0-195.3</td>
<td>180.8</td>
<td>13 (6.5%)</td>
<td>0</td>
</tr>
<tr>
<td>TOTAL</td>
<td>1803</td>
<td>18.5±0.6</td>
<td>17.2-20.7</td>
<td>182.7±6.7</td>
<td>162.0-205.5</td>
<td>182.7</td>
<td>241 (13.4%)</td>
<td>16 (0.9%)</td>
</tr>
</tbody>
</table>

Table 2 Skewness, kurtosis and tests of normal distribution in individual counties (županije).

Abbreviations: K-S test = Kolmogorov-Smirnov test; Sh-W test = Shapiro-Wilk test.

Figure 2 shows that the counties of Šibenik-Knin (183.4 cm), Dubrovnik-Neretva (183.6 cm) and Split-Dalmacija (184.1 cm) are by far the tallest and largely mirror average height documented by our previous study in the adjacent regions of Herzegovina – Canton 10/Livno (183.7 cm), Canton Western Herzegovina (184.0 cm), Canton Herzegovina-Neretva (182.8 cm) and the region of Trebinje (184.5 cm).
Remarkably, the anomaly in the area of Čapljina (185.9 cm) and Široki Brijeg (185.4 cm), where we found the tallest means in BiH, has an analogy on the Croatian side of the border in the towns of Metković (184.9 cm), Imotski (186.2 cm) and Makarska (187.6 cm) (Table 3). Although all the samples are relatively small (21-38 males), such a high frequency of extremely tall means within a small geographical area cannot be a mere coincidence. This suggests that the peak of male height should be sought in the area demarcated by Makarska – Imotski – Široki Brijeg – Čapljina - Metković.

<table>
<thead>
<tr>
<th>County (županija)</th>
<th>Town</th>
<th>Males</th>
<th>Females</th>
<th>Sex difference (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Av. height (cm)</td>
<td>n</td>
<td>Av. height (cm)</td>
</tr>
<tr>
<td>Split-Dalmacija</td>
<td>Makarska</td>
<td>27</td>
<td>187.6</td>
<td></td>
</tr>
<tr>
<td>Split-Dalmacija</td>
<td>Imotski</td>
<td>21</td>
<td>186.2</td>
<td></td>
</tr>
<tr>
<td>Dubrovnik-Neretva</td>
<td>Metkovic</td>
<td>39</td>
<td>184.9</td>
<td>27</td>
</tr>
<tr>
<td>Šibenik-Knin</td>
<td>Šibenik</td>
<td>51</td>
<td>184.2</td>
<td>32</td>
</tr>
<tr>
<td>Split-Dalmacija</td>
<td>Split</td>
<td>154</td>
<td>183.8</td>
<td></td>
</tr>
<tr>
<td>Dubrovnik-Neretva</td>
<td>Dubrovnik</td>
<td>135</td>
<td>183.7</td>
<td></td>
</tr>
<tr>
<td>Split-Dalmacija</td>
<td>Sinj</td>
<td>34</td>
<td>183.7</td>
<td></td>
</tr>
<tr>
<td>Zadar</td>
<td>Zadar</td>
<td>90</td>
<td>182.8</td>
<td></td>
</tr>
<tr>
<td>Primorje-Gorski Kotar</td>
<td>Rijeka</td>
<td>118</td>
<td>182.7</td>
<td></td>
</tr>
<tr>
<td>Šibenik-Knin</td>
<td>Knin</td>
<td>45</td>
<td>181.7</td>
<td></td>
</tr>
<tr>
<td>Istra</td>
<td>Pula</td>
<td>97</td>
<td>181.2</td>
<td>168</td>
</tr>
<tr>
<td>Karlovac</td>
<td>Karlovac</td>
<td>97</td>
<td>180.8</td>
<td>114</td>
</tr>
<tr>
<td>Karlovac</td>
<td>Ogulin</td>
<td>33</td>
<td>180.2</td>
<td>22</td>
</tr>
<tr>
<td>Lika-Senj</td>
<td>Gospić</td>
<td>22</td>
<td>179.1</td>
<td></td>
</tr>
</tbody>
</table>

Table 3 Average male and female height in 14 individual towns according to the self-reported place of residence. Only towns with at least 20 measured individuals are included.

In the direction to the north of this area, height begins to decrease quite rapidly, although this change is not always evident at the level of individual towns. The average of the Šibenik-Knin county (183.4 cm) is 0.7 cm lower than in the Split-Dalmacija county, but boys from Šibenik are still very tall (184.2 cm), taller than boys in Split. A similarly high mean was found in the school in Drniš (184.4 cm, n=42), which is situated approx. 35 km far inland. In fact, a small sample of boys resident in Drniš (186.6 cm, n=15) reached almost the same average height as the sample of Pineau et al. mentioned above (187.0 cm). However, two schools in Knin, which is approx. 25 km further inland, were much shorter (182.8 cm, n=39) and a sample of boys resident in Knin reached only 181.7 cm. We cannot exclude the possibility that these large differences between coastal and inland regions are due to relatively small sample sizes, but the same findings were previously reported even by Prebeg (1988) and ascribed to economic factors.
Height further drops by 0.6 cm in the county of Zadar (182.8 cm) and this drop again appears to be more pronounced inland, as indicated by the school of Gračac (178.8 cm, n=13). Still, it should be mentioned that the area of Gračac is very sparsely populated and it is very difficult to collect samples, which would be adequately representative. In addition, the local population consists of many Croatian immigrants from BiH, who may not have the same genetic background.

In the county of Lika-Senj, the decrease of height is relatively the most dramatic (by 1.8 cm to 181.0 cm), but considering that there are only five high schools in this sparsely populated and mountainous region, the final result may have been significantly influenced by the absence of Gimnazija Gospić that refused to participate in the survey. In fact, the average of the town of Gospić, based overwhelmingly on boys from the local vocational school (Strukovna škola) was only 179.1 cm, which seems too low. Understandably, boys from a vocational school represent the bottom end of the social spectrum, while boys from gimnazija represent the upper end, and hence the mean of the whole county may be underestimated. If we exclude boys from Strukovna škola Gospić, the average of boys resident in the Lika-Senj county would be 181.9 cm (n=49), which is in line with the average of the Primorje-Gorski Kotar county (181.9 cm) bordering the northwest.

It is noteworthy that 118 boys residing in Rijeka – the capital of the Primorje-Gorski Kotar county – were quite tall (182.7 cm), matching their peers in northern Dalmatia. Other towns were not represented by a sufficient number of boys, but at least those from the neighbouring Viškovo (181.4 cm, n=16) confirm the usual height standard in this region. In the county of Istra (the Istria peninsula), height decreases by 0.8 cm to 181.1 cm, although this result has certain limitations, because it was based on eight schools in a single town (Pula). However, the total picture indicates that height averages remain quite high (>181 cm) in all the coastal areas surrounded by the mountain ridges of the Dinaric Alps. Across the Velika Kapela ridge, the height mean falls quite markedly by 1.3 cm to 180.6 cm in the mainland county of Karlovac. This is already a value that is not far from the mean of boys from Zagreb (180.1 cm) mentioned in the introduction to this paper.

**Female height.** The average height of 782 girls from 28 schools was 167.4±6.2 cm. Regional differences were relatively large (2.5 cm), but lower than in males: from 166.6 cm in the county of Karlovac to 169.1 cm in the county of Dubrovnik-Neretva. However, some samples
(especially those from the counties of Lika-Senj, Zadar and Dubrovnik-Neretva) were very small, below 50 individuals. Still, all the women’s samples have a normal distribution of values. Only the small sample from the county of Zadar (n=20) approaches a significantly abnormal distribution according to the Shapiro-Wilk test (p=0.07), which is mainly due to high kurtosis (1.68), i.e. a high concentration of values around the mean.

<table>
<thead>
<tr>
<th>County (županija)</th>
<th>n</th>
<th>Age (years) Average (SD)</th>
<th>Range</th>
<th>Height (cm) Average (SD)</th>
<th>Range</th>
<th>Male height Average (SD)</th>
<th>Difference (men-women)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Split-Dalmacija</td>
<td>148</td>
<td>18.5±0.5</td>
<td>17.8-20.4</td>
<td>168.9±5.9</td>
<td>151.5-186.0</td>
<td>184.1±6.9</td>
<td>15.2</td>
</tr>
<tr>
<td>Dubrovnik-Neretva</td>
<td>39</td>
<td>18.4±0.2</td>
<td>18.0-19.0</td>
<td>169.1±7.1</td>
<td>156.2-188.0</td>
<td>183.6±6.7</td>
<td>14.5</td>
</tr>
<tr>
<td>Šibenik-Knin</td>
<td>74</td>
<td>18.9±0.6</td>
<td>17.9-19.9</td>
<td>167.9±5.1</td>
<td>156.0-179.2</td>
<td>183.4±6.6</td>
<td>15.5</td>
</tr>
<tr>
<td>Zadar</td>
<td>20</td>
<td>18.4±0.5</td>
<td>17.3-19.1</td>
<td>167.5±6.9</td>
<td>151.4-183.0</td>
<td>182.8±6.2</td>
<td>15.3</td>
</tr>
<tr>
<td>Primorje-Gorski Kotar</td>
<td>5</td>
<td>18.4±0.3</td>
<td>18.1-18.8</td>
<td>168.8±5.5</td>
<td>161.7-178.3</td>
<td>181.9±6.7</td>
<td>13.1</td>
</tr>
<tr>
<td>Istra</td>
<td>225</td>
<td>18.5±0.5</td>
<td>17.1-20.8</td>
<td>166.7±6.7</td>
<td>148.2-182.6</td>
<td>181.1±6.7</td>
<td>14.4</td>
</tr>
<tr>
<td>Lika-Senj</td>
<td>48</td>
<td>18.5±0.4</td>
<td>18.0-20.1</td>
<td>168.0±5.4</td>
<td>152.3-180.2</td>
<td>181.0±6.8</td>
<td>13.0</td>
</tr>
<tr>
<td>Karlovac</td>
<td>223</td>
<td>18.5±0.4</td>
<td>17.5-20.0</td>
<td>166.6±6.0</td>
<td>151.2-181.3</td>
<td>180.6±6.2</td>
<td>14.0</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td><strong>782</strong></td>
<td><strong>18.6±0.5</strong></td>
<td><strong>17.1-20.8</strong></td>
<td><strong>167.4±6.2</strong></td>
<td><strong>151.2-188.0</strong></td>
<td><strong>182.7±6.7</strong></td>
<td><strong>15.3</strong></td>
</tr>
</tbody>
</table>

**Table 4 Average female height in individual counties (županije) according to the self-reported place of residence.**

After the correction for population size, the average female height would be 168.5 cm in Dalmatia, 168.3 cm in seven counties of Adriatic Croatia and 168.2 cm in all eight counties. In general, it seems that girls in counties with the tallest boys (around 184 cm) reach a height of approximately 169 cm (Table 4). This is a very tall mean, but not as tall as in the young women aged 20-21 years in the Netherlands (170.5 cm) (Schönbeck et al., 2012) and shorter than the results of Pineau et al. (2005) from Split (171.1 cm, n=873) and Drniš (174.3 cm, n=42). In the present study, we found only one school with a mean height over 170 cm - Gimnazija Imotski (170.5 cm, n=24). The only female sample measured by Pineau et al. which stands close to our results is that from Dubrovnik (169.4 cm, n=259).

**Relationship between male and female height.** The unexpectedly shorter height of girls is accompanied by an unusually large difference in mean height between boys and girls in the eight counties, reaching 15.5 cm in the county of Šibenik-Knin and 14.4 cm on average (when comparing means corrected for population size). Even if we compare samples that are most representative (Istra, Karlovac), the sex difference is still 14.4 and 14.0 cm, respectively. At the same time, the usual difference in Europe is only 13 cm (Steckel, 1996).
Table 5 summarizes sex variation in height in the eight countries/territories on the territory of the Dinaric Alps. The discrepancy is similarly high, reaching 14.5 cm in Serbia, and the values of men and women strongly correlate with each other (r=0.97, p<0.001). Although the difference between male and female height increases as the population mean increases, we found that in our unpublished sample of 141 countries/territories, from which male and female data on height are available, the mean sex difference ranges between 11-12 cm in short-statured nations to 13-14 cm in tall-statured nations, with a global mean of 12.4 cm. The gap is only 13.1 cm even in the world’s tallest nation – the Dutch. Therefore, the sex differences between men and women in former Yugoslavia appear to be larger than the global trend line predicts (Fig. 3).

<table>
<thead>
<tr>
<th>Country/region</th>
<th>Date</th>
<th>Age</th>
<th>Male height (cm)</th>
<th>Female height (cm)</th>
<th>Sex differ. (cm)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Croatia</td>
<td>2006-08</td>
<td>18</td>
<td>180.5</td>
<td>166.3</td>
<td>14.2</td>
<td>Jureša et al. (2012)</td>
</tr>
<tr>
<td>Montenegro</td>
<td>2013</td>
<td>17-20</td>
<td>183.4*</td>
<td>169.4*</td>
<td>14.0</td>
<td>Popović (2017)</td>
</tr>
<tr>
<td>Kosovo</td>
<td>2016</td>
<td>17-18</td>
<td>179.5</td>
<td>165.7</td>
<td>13.8</td>
<td>Popović et al. (2017)</td>
</tr>
<tr>
<td>Slovenia</td>
<td>2012</td>
<td>18-21</td>
<td>179.8</td>
<td>166.5</td>
<td>13.3</td>
<td>G. Starc 2013 – pers. comm.</td>
</tr>
<tr>
<td>Macedonia</td>
<td>2012</td>
<td>18</td>
<td>177.4</td>
<td>164.5</td>
<td>12.9</td>
<td>Gontarev et al. (2014)</td>
</tr>
<tr>
<td>Albania</td>
<td>2008-09</td>
<td>20-29</td>
<td>174.0</td>
<td>161.8</td>
<td>12.1</td>
<td>IS &amp; IPH Albania &amp; ICF Macro (2010)</td>
</tr>
</tbody>
</table>

*Note: These values would decrease to 182.9 cm and 168.8 cm, respectively, if we took population size in individual regions into account.
Body proportions. Information on body proportions is available for only 209 boys. The majority (n=121) came from the northern part of the Adriatic coast (counties Istra, Primorje-Gorski Kotar and Karlovac). The remaining ones (n=88) resided in the southern part (counties Dubrovnik-Neretva and Split-Dalmacija) and were measured at Pomorska škola in Dubrovnik. Despite this limitation, the results are interesting, because when combined with our previous data from BiH, they indicate geographical trends in body proportions (Table 6).

The boys from the southern region have height and body proportions that are virtually indistinguishable from boys in Herzegovina – tall stature around 184 cm, relatively long legs (52.0-52.1% body height) and relatively short arms (100.3% body height). Anthropometric characteristics of boys in the northern region are similar to those of boys from Bosnia – much shorter height (180.5-180.7 cm), higher relative sitting height (52.3-52.5%) and higher
relative arm span (100.6-101.6%). The differences in relative sitting height are not significant between the two Croatian regions (p=0.14), but those in relative arm span are (p<0.001).

<table>
<thead>
<tr>
<th>Age (years)</th>
<th>n</th>
<th>Av.height (cm)</th>
<th>Sitting height (cm)</th>
<th>Sitting height (% height)</th>
<th>Arm span (cm)</th>
<th>Arm span (% height)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bosnia</td>
<td>1399</td>
<td>180.7±6.7</td>
<td>94.8±3.3</td>
<td>52.48±1.30</td>
<td>181.9±7.7</td>
<td>100.6±2.2</td>
</tr>
<tr>
<td>Adriatic coast (North)1</td>
<td>121</td>
<td>180.5±5.9</td>
<td>94.4±3.0</td>
<td>52.32±1.32</td>
<td>183.5±8.1</td>
<td>101.6±2.7</td>
</tr>
<tr>
<td>Adriatic coast (South)2</td>
<td>88</td>
<td>184.3±6.6</td>
<td>95.9±3.4</td>
<td>52.04±1.30</td>
<td>184.8±7.6</td>
<td>100.3±2.4</td>
</tr>
<tr>
<td>Herzegovina</td>
<td>451</td>
<td>184.1±7.2</td>
<td>95.9±3.4</td>
<td>52.11±1.63</td>
<td>184.6±8.3</td>
<td>100.3±2.3</td>
</tr>
</tbody>
</table>

Table 6 Male height and body proportions on the Adriatic coast of Croatia and in Bosnia and Herzegovina (according to the self-reported place of residence).

Notes: 1Counties Istra, Primorje-Gorski Kotar and Karlovac. 2Counties Dubrovnik-Neretva and Split-Dalmacija.

Information on body proportions was also collected in 171 girls coming from the counties of Istra, Primorje-Gorski Kotar and Karlovac. Their height was 166.2±6.6 cm, sitting height 88.8±3.6 cm and arm span 165.9±7.3 cm. Their relative sitting height (53.4±1.5%) and relative arm span (99.9±2.2%) significantly differed from boys residing in the same counties (p<0.001) and pointed to much shorter limb length relative to stature. The fact that women have relatively shorter limb length than men is well documented (Eveleth & Tanner, 1976).

Socioeconomic factors. Similar to our previous study in BiH, we collected information on the education of parents. These self-reported data were available in 1708 boys and 634 girls. In contrast with the results in BiH, where sons of university educated parents were 1.9 cm taller than sons of parents without university education, in the present study we found a much smaller disparity in this regard (0.5 cm: 183.1 cm vs. 182.6 cm), which was not significantly different (p=0.28). The smaller magnitude of this difference was also indicated by the fact that elite high schools (gimnazija) were not as often among the tallest schools as in BiH. The results were somewhat more pronounced in girls (1.1 cm: 168.1 cm vs. 167.0 cm), although they did not reach significance either (p=0.18). At the same time, the percentages of boys and girls in each category of parents’ education were very similar, which suggests that these self-reported data can be regarded as very trustworthy (Table 7).
Parents (university education) | Males | | Females |
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>% total</td>
<td>Av. height (cm)</td>
<td>n</td>
<td>% total</td>
<td>Av. height (cm)</td>
</tr>
<tr>
<td>Neither parent</td>
<td>1,038</td>
<td>60.8</td>
<td>182.6</td>
<td>404</td>
<td>63.7</td>
<td>167.0</td>
</tr>
<tr>
<td>Father</td>
<td>459</td>
<td>26.9</td>
<td>182.8</td>
<td>155</td>
<td>24.4</td>
<td>167.6</td>
</tr>
<tr>
<td>Father only</td>
<td>226</td>
<td>13.2</td>
<td>182.5</td>
<td>76</td>
<td>12.0</td>
<td>167.1</td>
</tr>
<tr>
<td>Mother</td>
<td>443</td>
<td>25.9</td>
<td>182.8</td>
<td>154</td>
<td>24.3</td>
<td>167.9</td>
</tr>
<tr>
<td>Mother only</td>
<td>211</td>
<td>12.4</td>
<td>182.5</td>
<td>75</td>
<td>11.8</td>
<td>167.7</td>
</tr>
<tr>
<td>One parent</td>
<td>438</td>
<td>25.6</td>
<td>182.5</td>
<td>151</td>
<td>23.8</td>
<td>167.4</td>
</tr>
<tr>
<td>Both parents</td>
<td>232</td>
<td>13.6</td>
<td>183.1</td>
<td>79</td>
<td>12.5</td>
<td>168.1</td>
</tr>
</tbody>
</table>

Table 7 Relationship between the height of measured males & females and the university education of their parents.

Differences between urban and rural populations were insignificant as well (p>0.05). Urban boys from towns with 25,000+ inhabitants were 182.8 cm tall (n=761), boys from towns and villages with less than 25,000 inhabitants reached 182.6 cm (n=1042) and in towns and villages with less than 10,000 inhabitants 182.4 cm (n=743). Also, no differences were found among girls from the counties of Istra, Lika-Senj and Karlovac, where the female samples were most representative. Urban girls (166.7 cm, n=282) had the same height as girls from towns and villages with less than 10,000 inhabitants (166.6 cm, n=164).

Statistics of monthly netto/brutto salary (in kuna/HRK) and unemployment in the period 1995-2014, provided by the Croatian Bureau of Statistics (https://www.dzs.hr), did not produce any significant correlations with male height in eight counties (Supplemental Figs. S1-S4). The inclusion of these statistics into a regression model did not lead to any significant results either (data not shown). However, these comparisons indicate that relatively tall statures in Rijeka (the capital of the Primorje-Gorski Kotar county) could be explained by economic factors. The county of Primorje-Gorski Kotar has the second highest netto salary in Croatia (after the city of Zagreb) and the fourth lowest unemployment rate (after the city of Zagreb and the counties of Istra and Varaždin). In addition, the neighbouring county of Istra has the fourth highest netto salary in Croatia. Therefore, we can assume that height in these two counties is disproportionately elevated due to favorable economic conditions.

In contrast, the mountainous county of Lika-Senj has the lowest netto salaries among the eight examined counties. However, even this county is still ranked 11th out of 21 Croatian counties. In other words, eight out of top 11 Croatian counties with the highest netto salaries belong to the Adriatic region that we examined in the present study. This must undoubtedly be
attributed to the effect of tourism. Therefore, the impact of economic factors could potentially manifest if we compared counties of the Adriatic region with the rest of Croatia. Similar to Prebeg (1988), we can also suppose that the shorter statures documented in the inland of Dalmatia are due to the fact that the economic benefits of tourism are limited to the Adriatic coast.

**Nutrition.** The Croatian Bureau of Statistics was not able to provide any data on the regional food production or consumption, and hence our nutritional analysis depends only on crude national statistics of food supply from the FAOSTAT database. These data show that protein consumption in Croatia has dramatically increased since 1992 and most of this increase can be attributed to animal proteins (Fig. 4). The consumption of key proteins from dairy and pork in 2013 is almost twice as high as 1993.

However, this development apparently copies the trend of the GDP per capita, which decreased dramatically from 8907 USD in 1990 to 5803 USD in 1993 (-35%). The level of 1990 was surpassed as late as in 2002 (9026 USD) (The National Accounts Main Aggregates Database). Therefore, the current quality of nutrition in Croatia probably isn’t much higher than in the 1980s. Indeed, the ‘protein index’ (the ratio between high-quality animal proteins and low-quality plant proteins), which is the strongest dietary predictor of male height in Europe (Grasgruber et al., 2014), is still quite low in Croatia. In the present updated sample of 44 European countries, proteins from dairy & pork/wheat produce the highest correlation coefficients (Fig. 5). The Croatian mean for the period 1993-2013 is 1.07, which is below the European average (1.21). During the last decades, this index has increased only moderately, from 0.93 in 1992 to 1.30 in 2013, and has been basically stagnating since 2007. Therefore, when expressed by this index, the quality of nutrition in Croatia is still deeply suboptimal, which is a situation that has analogies even in other countries of the former Yugoslavia (Bosnia and Herzegovina, Macedonia, Serbia). Only Slovenia (1.56) and Montenegro (1.53) are above the European mean.
Figure 4 Average daily protein intake (supply) from major protein sources in Croatia between 1992-2013.

Figure 5 Relationship between male height and the "protein index" (the ratio between high-quality proteins from dairy and pork, and low-quality proteins from wheat) in 47 countries of Europe and overseas (FAOSTAT, 1993-2013).

Note: The graph contains updated values of male height: Greece (176.1 cm), Hungary (179.9 cm), Latvia (180.2 cm), Lithuania (179.4 cm), Malta (173.0 cm), Montenegro (182.9 cm), Norway (180.0 cm), Switzerland (178.4 cm), the United Kingdom (177.5 cm).

Genetics. The genetic aspects of the exceptional stature on the Adriatic coast are certainly the most interesting, but still supported only by a superficial genetic marker – frequencies of Y haplogroup I-M170 in the European context (Fig. 6). This mutation on the male Y chromosome can be linked with the Upper Paleolithic Gravettian culture and after the end of the Ice Age, it expanded from the ‘Epigravettian’ glacial refugium around the Adriatic sea (for a more detailed discussion, see our previous paper Grasgruber et al., 2017). All we can say at the moment is that North European populations carrying high frequencies of I-M170
indeed do carry single nucleotide polymorphisms (SNPs) associated with tall stature (Robinson et al., 2015).

Figure 6 Relationship between average male height and the frequency of Y haplogroup I-M170 in 44 countries of Europe & USA. Five regional samples from the former Yougoslavia are displayed for additional comparison.

Note: I-M170 frequencies in Bosnia, Herzegovina and Kosovo (Kosovar Albanians) were taken from Perićić et al. (2005). I-M170 frequencies in the Zadar county (‘Zadar hinterland’) and Dubrovnik were taken from Šarac et al. (2016).

Remarkably, regional data on I-M170 frequencies from Herzegovina, Bosnia, the Zadar county in Dalmatia and Dubrovnik (Perićić et al., 2005; Šarac et al., 2016) fit the relationship between height and I-M170 at the country level, although height is still lower than expected, especially in the case of the Zadar county. This can be explained by the very small size of the Zadar genetic sample (n=25). Only Kosovo is a clear exception, apparently due to the strong recent drift of Y haplogroup E1b-M78 in the local Albanians (Perićić et al., 2015).
DISCUSSION

To our knowledge, this study constitutes the most detailed report on the regional differences in stature on the Adriatic coast of Croatia since the 1980s. As already mentioned above, these differences reached 5 cm (166-171 cm) at the end of the 19th century and this range has largely persisted until today, because we documented a 3 cm gap (181.1-184.1 cm) between the counties of Istra and Split-Dalmacija. It is intriguing that height in individual counties mirrors the height in the neighbouring cantons of BiH. Therefore, if any local factors influence stature, they must work similarly on both sides of the border.

The peak of male height in the Dinaric Alps was observed in southern Dalmatia and the Croatian-speaking western Herzegovina, approximately in the area demarcated by the towns of Makarska – Imotski – Široki Brijeg – Ćapljina – Metković, where we encounter averages around 185 cm or higher. Another peak may exist in central and northwestern Montenegro, in the municipalities of Kolašin & Savnik (185.5 cm, n=30) and Plužine & Žabljak (184.9 cm, n=28) (Popović, 2017), but the samples are apparently very small. In the same survey, the tallest Montenegrin females were found in the northwestern municipalities of Nikšić (170.9 cm, n=204) and Plužine-Žabljak (170.1 cm, n=34), which are values that our female samples from Dalmatia cannot match. These results delimit regions, which can be targeted in future genetic studies aimed at more detailed investigation of the Dinaric phenomenon.

Although the Dutch are still officially the tallest nation in the world with averages of 183.8 cm in men and 170.5 cm in women (if we pool the means of 20-21 year olds) (Schönbeck et al., 2012), it should be noted that the average is only 182.4 cm and 169.7 cm in the age category of 18 years, and 183.6 cm and 170.1 cm in the age category of 19 years. The size of the samples is also quite small (only 211 males and 215 females aged 20-21 years) and it is not entirely clear, if the samples past high-school age (18+ years) are not artificially elevated due to the inclusion of university students (as mentioned in the ‘Methods’ section of that paper). Therefore, these data from the Netherlands cannot be perfectly compared with our data from the Balkans, where we targeted males and females aged 17-20 years, with a preponderance of 18-year olds. In fact, both 18-year old boys from Dalmatia (n=839) and Herzegovina (n=632) reach 183.6 cm, and Dalmatians would be even slightly taller than Herzegovinians, if we took population size in regions into account. Although the mean height of Montenegrin boys aged 17-20 years is only 182.9 cm, when corrected for regional population size, they may also be taller than their Dutch peers.
Figure 7 shows that the area with tall statures above 181 cm roughly copies the outer mountain ridge of the Dinaric Alps. Only the region of Bijeljina in northeastern Bosnia is an exception, possibly due to good economic conditions. Areas with the tallest statures above 182 cm lie on the inner side of the ridge in Herzegovina, Dalmatia and central/northwestern Montenegro. This picture shows that height in the Dinaric Alps is not connected with the limestone bedrock *per se*, which would not support the hypothesis of Coon (1970), who speculated that height in North Albanians living on limestone is elevated due to the high mineral content in the food chain. Rather, height peaks behind the mountain range, which historically served as a barrier to genetic flow. Interestingly, the height of contemporary Albanian men is only 174.0 cm, which is 8.9 cm shorter than in Montenegrins, and 5.5 cm shorter than in Kosovar Albanians. Preliminary results from Albanian universities confirm that these large differences are real (S. Popović, 2017 – pers. communication). Because the quality of nutrition in Albania appears to be similar to that of BiH, Croatia, or Serbia, and the GDP per capita in Kosovo (for 2016) is 18% lower than in Albania (The World Bank), this remarkable phenomenon deserves further research.

It is striking that we cannot again confirm the results by Pineau et al. (2005) from the years 2001-2003, who reported a higher male height in Herzegovina (+1.6 cm) and mostly higher male and female means in the individual regions of Dalmatia. The authors list a mean male height of 183.1 cm in the schools of Dubrovnik (n=259), 184.5 cm in Split (n=875) and 187.0 cm in Drniš (n=21). We found a mean height of 183.6 cm in the schools of Dubrovnik (n=172), 183.6 cm in Split (n=228) and 184.4 cm in Drniš (n=42). Even more importantly, our data cannot support the mean height of girls in Dalmatia, who reached 171.1 cm in Split (n=873) – approximately 2 cm more than in the present study.
As already mentioned (Grasgruber et al., 2017), Pineau et al. collected at least some of their data in Herzegovina and Dalmatia via personal communication with the local physical education teachers, which could influence their results. Furthermore, the secular trend of youths in Tuzla schools was not negatively affected by the Bosnian war (1992-1995) and continued at a relatively fast rate (Grasgruber et al., 2017; Hadžihalilović et al., 2006), so we do not suppose that height in other regions of BiH would decrease, especially considering the fact that boys measured during our survey in BiH were growing up after the end of the war. Nevertheless, recent evidence shows that height in some Croatian regions may have really decreased during the last two decades.

The events of the Croatian war of independence (1991-1995) clearly influenced the growth of children in Osijek in eastern Croatia, because 7-8 year olds measured in 1995-1996 were
approximately 2 cm shorter than their peers measured in 1980-1981 (Jovanović et al., 2003). Older birth cohorts developed normally. In Zagreb, the research of the Andrija Štampar School of Health between 1951-1991 documented a continuous, positive height trend (Fig. 8) (Prebeg et al., 1995). However, studies of the Institute for Anthropological Research between 1991-2010 showed a significant decrease from 180.7 cm to 180.1 cm in boys and from 167.1 cm to 165.2 cm in girls (Petranović et al., 2014). Although these two institutions apparently targeted different types of schools and the latter surveys were less representative, it is clear that no increase of height has occurred in Zagreb since 1991. This development can be connected with the dramatic decline of the economy in the early 1990s, which recovered as late as during the 2000s.

**Figure 8** Development of the secular trend in the city of Zagreb between 1951-2010. Pooled averages of 18 and 19 year olds. Based on the studies of the Andrija Štampar School of Health (Jovanović et al., 2003) and the Institute for Anthropological Research (Petranović et al., 2014).
Still, the mean height of 18-year olds in Croatia has increased by 2.9 cm in boys and 1.8 cm in girls between 1980-84 and 2006-08 (Jureša et al., 2012). Historical data show that between 1883-2008 (125 years), the average Croat male has grown by 15 cm (from 165.5 cm to 180.5 cm), which means an average rate of 1.2 cm/decade. Based on the information listed by Coon (1939), we can estimate that the height gain of young men in the county of Istra has been approximately 15 cm as well. According to the records of Austrian-Hungarian recruits around the year 1870 (Komlos, 2007), young men from the town of Zadar (Zara) were the tallest in the whole empire at 168.7 cm, which is a difference of +14.1 cm, when compared to the present study (1.0 cm/decade). However, it should be noted that these historical data do not necessarily represent the same populations, due to migrations to the coastal regions occurring in the course of the 20th century.

Historical information from other regions of the Adriatic area is scarcer. As already mentioned, the most recent nationwide survey comparable with the dimension of our work was conducted in 1980-1984 (Prebeg, 1988). Another nationwide survey was performed in 1991-1993, but was limited to a mere four areas (Prebeg, 1998). Very few detailed numbers from these studies were published, but some rough data on Split are available (Jovanović et al., 2003). They show that in 1980-1984, the mean height of 18-year olds in Split was 181 cm in boys and 167 cm in girls. In 1992, it reached 182.5 cm and 170 cm, respectively. Although the height of girls from the latter survey appears unlikely high, these values show that at least in boys, the secular trend was continuing even during the subsequent economic depression. This could explain why the nationwide average increased as well, despite possible stagnation or decline in Zagreb and other areas of mainland Croatia. Still, our present study indicates that these economic disturbances may have eventually affected even Dalmatia since 2001-2003.

CONCLUSION

In summary, the data presented in our article demonstrate that people from Dalmatia currently belong to the tallest in the world, and local young men are even the tallest in the age category of 18 years. However, this phenomenon is limited only to the territory of Dalmatia, Herzegovina and Montenegro. Other regions of Croatia are characterized by a much shorter stature and these large regional differences have persisted at least since the end of the 19th century. The taller statures in Adriatic Croatia can be, at least partly, linked with more favourable economic conditions, but these factors cannot explain, why the north-to-south gradient is very similar both in Adriatic Croatia and in BiH, on both sides of the mountain
range forming a natural border between these two countries. Because we are not aware of any environmental factor that could be responsible for these geographical trends, specific genetic predispositions shared by these populations are the most likely explanation. On the other hand, the striking shortness of Albanians, when compared to the neighbouring Montenegrins and Kosovar Albanians, represents a different kind of extreme, which would require clarification in future studies. Another fundamental finding is the fact that the secular height trend in Croatia has been negatively influenced by the economic depression in the 1990s. The onset of the economic crisis in 2008 further delayed a marked improvement in living standards. However, because the quality of nutrition in Croatia is still below the European standards, a further continuation of the positive height trend is still possible. In the near future, we would want to cover even the rest of mainland Croatia and describe regional differences across the whole country.
REFERENCES


ADDITIONAL INFORMATION AND DECLARATIONS

Funding
This study was realized within the project "Anthropological research of sports potential in Dalmatia" number MUNI/A/1090/2016 with the support of the Specific University Research Grant, as provided by the Ministry of Education, Youth and Sports of the Czech Republic in the year 2016.

Ethics statement
The project and all the planned procedures were approved by the Ethics committee of the Faculty of Sports Studies, Masaryk University Brno, under the reference number EKV-2016-094. The Ethics committee assessed the project and found no contradictions with applicable rules, regulations and international guidelines for biomedical research involving human participants. The research was subsequently approved by the Ministry of Education in Croatia, but the final approval depended on individual school directors and their agreement with the students' parents. Before the measurements, the examined students were acquainted with the objectives of this project and its ethical issues, and signed an informed consent.

Competing interests
The authors declare no conflict of interest.

Author contributions
- Pavel Grasgruber coordinated the study, conducted the fieldwork and drafted the manuscript
- Jan Cacek managed and supervised the study
- Stevo Popović co-wrote the manuscript
- Stipe Prce, Nikola Stračárová, Eduard Hrazdira, Sylva Hřebíčková, Predrag Potpara and Ivan Davidović conducted the fieldwork.

Supplemental information
Supplemental tables and figures
Supplemental dataset