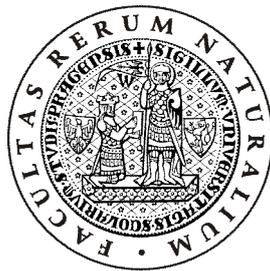


UNIVERZITA KARLOVA V PRAZE

P ÍRODOV DECKÁ FAKULTA



Dizertací práce

Praha 2012

Mgr. Lucie Bigoni

UNIVERZITA KARLOVA V PRAZE
PÍRODOV DECKÁ FAKULTA
KATEDRA ANTROPOLOGIE A GENETIKY LOV KA



**Fenotypová variabilita skeletu:
asymetrie, pohlavní dimorfismus
a jejich proměny v čase**

**Phenotype variability of the skeleton:
asymmetry, sexual dimorphism and their changes in time**

Dizertační práce

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Program: Biomedicína

Obor: Antropologie a genetika lov ka

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Praha 2012

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V Praze dne 30. kv- tna 2012

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Mojí milované rodin

Philippovi, Athurovi, Theovi, Felixovi

a tomu malému, který v-echno absolvoval se mnou.

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Abstrakt

Tato dizertá ní práce je p edkládána ve form svazku odborných publikací a konferen ních p ísp vk spolu s teoretickým úvodem. Prezentuje r zné pohledy na hodnocení variability lebky (pop . postkraniálního skeletu), s d razem na sledování diachronních zm n, asymetrie a pohlavního dimorfismu.

P edkládaná práce se soust e uje na klasickou morfometrickou i geometricko-morfometrickou analýzu tvarových a velikostních charakteristik lebky, kostí kon etin a obli eje u soubor pocházejících z populací flijících na území eské republiky. Prvním souborem je fotografická dokumentace svrchn paleolitických lebek z P edmostí u P erova (stá í 25 - 27 000 let). Druhý materiál p edstavují lebky a kosti kon etin pocházející z ran st edov kého sídli-t v Mikul ících (období Velké Moravy, 9. ó 10. století). T etí soubor pochází z Prahy z 30. let 20. století, tzv. Pachnerova sbírka. Posledním, zejména srovnávacím vzorkem populace, jsou RTG snímky lebek a 3D modely obli ej sou asné eské populace.

Studium kosterní asymetrie populací (Bigoni et al., v recenzním ízení, 2005; Kujanová et al., 2008), jejího stupn a lokalizace, umohl uje porovnávat r zné modely chování, flivotní podmínky, socioekonomické rozdíly a variabilitu uvnit a mezi populacemi (Mikul íce vs. Pachnerova sbírka). Direkcionální asymetrie poukazuje na asymetrické pouffívání kon etin i flvýkacího aparátu v d sledku preference jedné strany pro dané innosti. Fluktua ní asymetrie odráflí environmentální stres a schopnost populace na n j reagovat.

Výsledky potvrzují vysoký biomechanický a environmentální stres u Pachnerovy kolekce pocházející z nejnižších socioekonomických vrstev. Dále poukazují na socioekonomické rozdíly mezi různými oblastmi Mikulického sídliště a mezi pohlavími.

Pohlavní dimorfismus tvaru a velikosti byl sledován na lebce a obličejové části dospělé populace 20. a 21. století (Bigoni et al., 2010 a; Velemínská et al., 2012). Tvarové pohlavní rozdíly lebky nebyly zaznamenány na lebce jako celku, na lebeční bazi a celkovém tvaru neurokrania, signifikantní pohlavní dimorfismus tvaru byl zaznamenán v oblastech mediální části neurokrania, horního obličejového regionu obočnice, nosního otvoru a patra. Nejvýrazněji se projevoval ve tvaru horního obličejového, nasolabických obloučích. Celkový pohlavní dimorfismus obličejové je dán alometrickým vztahem jeho tvaru a velikosti. Nejvýrazněji se pohlavní dimorfismus lebky a obličejové projevuje v oblasti dolní části obličejové, zejména brady a nasolabických obloučích. Pohlavní rozdíly na obličejové jsou zejména v oblasti čela, obočnice a nasolabických obloučích, nosu a nosního otvoru, rtů a v celkových délkových parametrech.

Diachronní změny morfologie lebky byly sledovány v časovém horizontu svrchní paleolit až raný středověk až po začátek 20. století a současnost (Velemínská et al., 2008 a, 2009; Bigoni et al., 2010 b). Interpopulační variabilita v tomto případě ukázala zejména na trend k rozvoji neurokraniální globularity a snížení faciální konvexity. Tyto změny byly výraznější s rostoucí časovou vzdáleností populací.

Abstract

This doctoral thesis is submitted in the form of science publications and conference presentations together with theoretical introduction. It presents several points of view on the variability evaluation in the skull (and postcranial skeleton), with accent on diachronic changes monitoring, asymmetry and sexual dimorphism.

This study concentrates on analysis (using traditional and geometric morphometrics) of size and shape of the skull, limb bones and face in the samples originated in the region of the Czech Republic (Central Europe). The first one is a photographic documentation of the Upper Palaeolithic skulls from Předmostí near Přerov (age 25,000 - 27,000 years). The second material is represented by skulls and limb bones deriving from the Early Mediaeval settlement in Mikulčice (The Great Moravia, 9th to 10th century). The third sample originated in the 1930s in Prague, so called Pachner Collection. The last comparative sample presents radiographs of the head and 3D surface models of faces of the recent society.

Study of skeletal asymmetry of populations (Bigoni et al., v recenzním řízení, 2005; Kujanová et al., 2008), its level and localization, enables us to compare behavioral patterns, living conditions, socioeconomic differences and variability within and between populations (Mikulčice vs. Pachner Collection). Directional asymmetry adverts to asymmetrical using of limbs or masticatory apparatus in consequence of one side preference for some tasks. Fluctuating asymmetry reflects environmental stress and the ability of population to react.

Results confirmed high biomechanical and environmental stress in the Pachner Collection deriving from the lowest socioeconomic groups. Furthermore it refers to socioeconomic differences between different regions of Mikul ice settlement and between sexes.

Sexual dimorphism of the shape was evaluated in the skull and face of the Czech adult population from 20th and 21st century (Bigoni et al., 2010 a; Velemínská et al., 2012). Skull sexual differences were not found in the skull as a whole, in the cranial base and the shape of neurocranium, significant sexual dimorphism was noted in the regions of the midsagittal curve of neurocranium, upper face, orbits, nasal and palatal region. It was the most expressive in the shape of upper face, in the zygomatic arches. Sexual dimorphism of the face is presented of allometric relationship its shape and size. Sexual dimorphism manifests itself the most in the lower part of the face, especially in the chin, and also in the cheeks. Sexual differences were also apparent in the forehead region, orbits, and eyebrow ridges, nose and mouth aperture, in general in length-width parameters.

Diachronic changes of the skull morphology were monitored in the time horizon Upper Paleolithic ó Early Middle Ages ó the early part of the 20th century ó recent time (Velemínská et al., 2008 a, 2009; Bigoni et al., 2010 b). Towards recent inter-population variability confirmed the tendency to the development of neurocranial globularity and the decrease of facial convexity. These changes were more expressive with the increasing time interval between populations.

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Kapitola 1

Úvod

Tato dizertační práce je předkládána ve formě svázaných odborných publikací a konferenčních příspěvků spolu s teoretickým úvodem. Je prezentací různých přístupů k hodnocení variability lebky (popř. postkraniálního skeletu), s důrazem na asymetrii a pohlavní dimorfismus. Úvodní kapitola pojednává o biologické variabilitě lidských lebek z hlediska fenotypu, je zaměřena na syntézu jednotlivých předkládaných studií. Současně se zde zabýváme také jednotlivými studovanými populacemi, které všechny pochází v regionu České republiky a jsou tak významným spojovacím článkem všech zmiňovaných studií.

1.1 Fenotypová variabilita

Ke studiu biologické variability člověka přispívá zkoumání fenotypu i genotypu člověka. Na úrovni genotypu je každý člověk, s výjimkou jednovaječných dvojčat, jedinečný (Levy et al., 2007; Kidd et al., 2008). Na fenotypové úrovni, vlivem mnoha vnějších i vnitřních faktorů, je jedinečný každý z nás. Biologickou variabilitu lze sledovat v rámci jedné populace, ale je také

možné porovnávat mezi sebou různé, časově či geograficky vzdálené, populace. Přes pokrok v extrahování a sekvenaci fosilní DNA hraje kosterní morfologie stále klíčovou roli při studiu evoluce populací, adaptací na lokální klima či pro rekonstrukci vzájemné příbuznosti dávných i současných populací (Bruner et al., 2004; Betti et al., 2010).

Fenotypová variabilita je odrazem interakce našich genů se selektivními tlaky prostředí. Geografické rozložení fenotypové variability je výsledkem naší evoluční historie (Jobling et al., 2003; Relethford, 2009). Naše evoluční minulost bývá v dnešní době studována zejména na základě genotypu současné populace. Ten nám přibližuje i geografický původ člověka, nicméně podstata vzniku geografického rozdělení biologické variability člověka stále není jednoznačně objasněna (Cavalli-Sforza et al., 1994; Rosenberg et al., 2002; Serre and Pääbo, 2004; Wessen, 2005). Biologická variabilita skutečně do jisté míry koreluje s geografii a to jak u znaků pod vlivem přírodního výběru, tak u znaků selektivně neutrálních (Prugnolle et al., 2005; Relethford, 2009; Betti et al., 2010).

Mezi nejvýznamnější aspekty lidské variability patří rozmanitost v rámci kraniální morfologie. Analýza kraniofaciální morfologie hominidů je obzvláště důležitá při studování otázek zabývajících se fylogenetickými a ontogenetickými aspekty rodu *Homo* (Bernhard et al., 2002). Hlavní silou řídící formování moderní lidské lebky je proces encefalizace (Lieberman et al., 2000; Bruner et al., 2003). Některé jedinečné adaptace krku a hlavy (poloha očí, tvar lebeční baze, lokalizace foramen magnum, šijová oblast) jsou spojeny s jedinečně lidským způsobem vzpřímené polohy těla a bipedií (Lieberman, 2011). Dalším faktorem ovlivňujícím lebeční strukturu je také respirační adaptace vzhledem k bipedii a zkracování obličeje (Lieberman, 2011).

Lidská lebka sestává ze tří regionů s odlišným vývojovým původem a funkčními požadavky – lebeční baze, klenby a obličeje (Carlson, 1999). Baze je formována na základě enchondrální osifikace (Mooney et al., 2002), je to nejstarší struktura lebky a zůstává

relativně beze změn v průběhu fylogeneze (Carlson, 1999). Je pod výraznější genetickou kontrolou než klenba a obličej (Schilling and Thorogood, 2000; Sperber, 2001). Lebeční klenba je formována endesmální osifikací, vytváří prostor pro mozkové hemisféry (Sperber, 2001). Obličejový skelet osifikuje z většiny endesmálně, obklopuje hltan, ústní, dýchací a oční dutiny (Sperber, 2002). Environmentální faktory mají významný vliv na tvar obličeje, zatímco lebeční klenba a baze zůstávají relativně stabilní, s vysokým stupněm dědičnosti (Wood and Lieberman, 2001; González-José et al., 2005; Stynder et al., 2007). Důvodem je významná role obličejové části při výživě, adaptaci na prostředí a také proto, že faciální růst je prodloužen déle do postnatální periody (Siebert and Swindler, 2002). Podle Carson (2006) jsou nejméně dědičné znaky na obličejí a šířka lebky.

Ačkoliv předmětem výzkumu zůstává, do jaké míry je variabilita dána neutrálními procesy (genetickým driftem) či přírodním výběrem v souvislosti např. s klimatem, je zřejmé, že neutrální procesy mají mnohem větší vliv na formování lidské lebky než klima (Betti et al., 2010). Mnoho studií nezaznamenalo významnější spojení mezi klimatem a kraniální morfologií (Relethford, 2004; Roseman and Weaver, 2007; Betti et al., 2009, 2010). V rámci nezávislých proměnných (tvar a velikost krania, klima, neutrální znaky) je pouze tvar lebky signifikantně korelován s interpopulačními rozdíly v robusticitě lebky (Baab et al., 2010). Nicméně u některých částí obličeje, zejména v oblasti nosu, byly prokázány známky adaptace na chladné klima, avšak jen u populací žijících v extrémních podmínkách (Roseman, 2004; Roseman and Weaver, 2004; Harvati and Weaver, 2006). U těchto populací je termoregulační hypotéza spojována také s trendem pro brachycefalizaci (Beals et al., 1984).

Významný vliv na růst lebky má mastikace. Vzhledem k tomu, že žvýkání je opakované, frekventované a vyžaduje přesnost a sílu, není s podivem, že mnoho kraniofaciálních znaků odráží adaptaci na působení a odolávání těmto silám (Lieberman, 2011). S rozvojem žvýkacího aparátu a typem stravy dané populace souvisí robusticita lebky,

zejména maxillomandibulárního komplexu (Carlson and Van Gerven, 1977). Podle jiných autorů není robusticita přímo spojena s mastikací, neboť skupiny živící se na žvýkání náročnou stravou neprojevovaly větší robusticitu (Baab et al., 2010). Ta byla spíše spojena s tvarem lebky charakterizovaným delší mozkovnou, rozvinutou glabelární a okcipitální oblastí a větší faciální prognácií (Baab et al., 2010).

Efekt negativního environmentálního vlivu, jako je např. nedostatečná strava, vede k redukci velikosti lebky a změně jejího tvaru, neboť kosterní tkáň je citlivá na tyto vlivy, a to obzvláště v průběhu jejího vývoje (Larsen, 2002; Ruff, 2002; Stynder et al., 2007). Změna kraniofaciální velikosti a s tím spojená alometrická změna tvaru, soustředěná na oblast obličeje a frontálního regionu, je spojena s rostoucí velikostí populace, s nedostatkem zdrojů a s intenzifikací zemědělství (Henneberg and Steyn, 1993; Brown and Maeda, 2004; Sardi et al., 2004, 2006; Stynder et al., 2007). Chronický nutriční a jiný nespecifický stres se na lebce odráží také např. v podobě cribra orbitalia či hypoplázie zubní skloviny (Pfeiffer, 2007).

Kraniální znaky nesou informaci vhodnou k rekonstrukci historie populací, k výzkumu genového toku a genetické podobnosti (Relethford, 2004; Roseman and Weaver, 2004). Právě distribuce kraniálních znaků, se blíží rozložení znaků genetických (Relethford, 2005). Multivariační analýza kranio-metrické variability přinesla výsledky podobné těm získaným analýzou genetických markerů a DNA polymorfismů – 81% celkové variability se vyskytuje v rámci lokálních populací, pouze 6% variability existuje mezi lokálními populacemi a 13% mezi většími regiony (Relethford, 2002; Rosenberg et al., 2002). Selekcí tlaky lišící se mezi regiony tedy hrály pouze omezenou roli v celkové lidské kranio-metrické diverzitě (Relethford, 2005). Zároveň bylo popsáno, že fenotypová kranio-metrická podobnost klesá s rostoucí geografickou vzdáleností (Relethford, 2009). Fenotypová diverzita dosahuje, podobně jako genotypová, nejvyšších hodnot na Africkém kontinentu a směrem od něj postupně klesá (Relethford, 2002; Hanihara, 2008; Betti et al., 2010). Tento fenomén

podporuje představu relativně recentního vzniku moderního člověka v Africe a jeho následnou expanzi do ostatních částí světa. Některé studie však poukazují na multiregionální model vzniku anatomicky moderního člověka (Wolpoff, 1999; Wolpoff et al., 2000).

Další významnou složkou intra- a interpopulační variability jsou kosterní asymetrie a pohlavní dimorfismus. Pohlavní dimorfismus je výsledkem pohlavního výběru, různých genetických a strukturálních vlivů, souvisí s rozdílnou reprodukční a ekologickou rolí muže a ženy a jejich rozdílným chováním (Slatkin, 1984; Lieberman, 2011). Bilaterální asymetrie bývá používána ke zjišťování mechanismů vývoje a působení podmínek prostředí, neboť, na rozdíl od jediného vývojového původu symetrie, objevuje se bilaterální asymetrie ve fylogenezi mnohokrát (Ruppert and Barnes, 1994). Kraniofaciální asymetrie je důležitým indikátorem environmentálního stresu různého původu (Schaefer et al., 2006; DeLeon, 2007; Özener, 2010 a). O asymetrii, pohlavním dimorfismu a diachronních změnách lebky v rámci biologické variability člověka pojednávají následující kapitoly této práce.

Cílem publikací dotýkajících se kosterní asymetrie (lebky a kostí končetin) je stanovení rozsahu direkcionální a flukтуаční asymetrie, jejich lokalizace a velikosti, s ohledem na pohlaví. Účelem bylo sledování rozdílů v expresi asymetrie mezi raně středověkou a recentní populací v souvislosti s rozdílnými životními podmínkami a také v rámci středověké populace z hlediska socioekonomických rozdílů. Publikace s tématem pohlavního dimorfismu lebky má za cíl analyzovat pohlavní dimorfismus lebky identifikované série a ověřit použitelnost tvaru lebky a metod geometrické morfometrie k určení pohlaví a také lokalizovat oblasti lebky s nejvýraznějším tvarovým pohlavním dimorfismem. Předmětem studie zabývající se pohlavním dimorfismem obličeje je analýza vztahu mezi velikostní a tvarovou variabilitou pohlavních znaků obličeje pomocí 3D modelů obličejů současné české populace a zároveň odhalení a vizualizace rozdílů průměrného mužského a ženského obličeje. Ve studiích s tématem biologické variability lebky bylo naším

cílem nalézt diachronní změny a variabilitu velikosti a tvaru lebky středoevropské populace od svrchního paleolitu, přes raný středověk až po současnost s akcentem na nejtypičtější mikroevoluční změny *Homo sapiens*, jako je rozvoj neurokraniální globularity a snižování faciální konvexity.

1.2 Sledované populace

V předkládaných publikacích byla hodnocena variabilita u třech časově vzdálených populací se společným geografickým původem, přičemž předpokládáme jistou míru biologické kontinuity. Soustředíme se tedy na variabilitu člověka na území Čech a Moravy od svrchního paleolitu, přes raný středověk, počátek 20. století až po současnost.

1.2.1 Svrchní paleolit

První sledovaný soubor představuje fotografická dokumentace svrchně paleolitických lebek z Předmostí u Přerova. Kosterní pozůstatky téměř třiceti jedinců nalezené v Předmostí u Přerova patří mezi nejdůležitější světové nálezy anatomicky moderního člověka (Ferrie, 1997; Smith, 1997). Byly objeveny J. Wankelem, K. J. Maškou, J. Kniesem a M. Křížem v druhé polovině 19. století a K. Absolonem a J. Skutilem v první polovině 20. století společně s gravettienskými nástroji (Vlček, 1996). Jejich stáří je odhadováno na 25 - 27 000 let (Svoboda, 2001), jsou tudíž jedním z nejrozsáhlejších svrchně paleolitických souborů. Pohlaví fosilií bylo odhadováno v několika studiích (Matiegka, 1934; Šefčáková et al., 2003; Katina et al., 2004). Tento velmi homogenní soubor je právem považován za vzorek reprezentující celou populaci.

Antropologicky byl tento soubor poprvé hodnocen J. Matiegkou (1934, 1938). Výsledky zpracování byly publikovány ve 30. letech a od té doby je tento vzácný materiál používán jako referenční série v mnoha publikacích. Podle některých morfologických charakteristik je řazen k méně pokročilému typu moderního člověka než Cro-Magnon. Tento soubor bývá některými autory považován za spojovací článek mezi Neandertálci a současnými Evropany (Smith, 1997). Zároveň tyto fosílie slouží jako argument pro multiregionální model evoluce člověka (Wolpoff, 1999), popř. pro určitý stupeň dřívější příměsi neandertálské populace (Trinkaus and Svoboda, 2006).

Bohužel byl tento gravettienský soubor z Předmostí zničen při požáru Mikulovského zámku na konci 2. světové války. Jediným zdrojem informací o zničených skeletech tedy zůstává zmíněná Matiegkova publikace a sbírka profesionálně zhotovené fotodokumentace fosílií v podobě skleněných negativů. Lebky byly snímány za standardních podmínek, a tak je lze s vysokou reliabilitou hodnotit morfoskopicky i morfometricky (Velemínská and Brůžek, 2008). Odlitky lebek P3 a P4 a endokraniální odlitky P3, P4, P9 a P10 jsou uloženy ve sbírkách Moravského muzea v Brně (Jelínek and Orvanová, 1999). Objevení Matiegkovy původní dokumentace na skleněných negativech v posledních letech umožňuje nové zpracování kosterního vzorku 27 jedinců různého věku a pohlaví (Velemínská et al., 2004).

1.2.2 Raný středověk

Druhou v dizertaci použitou kolekcí je unikátní archeologický materiál, představující raně středověkou populaci z Mikulčic uloženou v depozitářích Antropologického oddělení Národního Muzea. Sídliště Mikulčice je považováno za jedno z nejvýznamnějších center Velké Moravy. Tento první historicky dokumentovaný slovanský státní útvar, datovaný do 9. - 10. století našeho letopočtu (Pouлік, 1975; Havlík, 1978), stál politicky a kulturně na pomezí

Byzance, Říma a Francké říše (Poláček, 2008). Velká Morava zahrnovala území jižní Moravy, Čech, jižního Polska, západního Slovenska a okolí řek Dunaje a Tisy. Během tohoto období dochází k přijetí křesťanství nejprve vládnoucí třídou (např., Třeštík, 2001; Poláček, 2008). Rozšíření křesťanství do nižších tříd nebylo tak rychlé, (Ohler, 2001; Smetánka, 2004); vliv na pohřební rituál a zejména hrobovou výbavu přes všechny socioekonomické třídy se projevil až v druhé polovině 9. století (Třeštík, 2001; Poláček, 2008). Během 10. století byla Velká Morava obsazena a zničena vpádem Maďarů (Poláček, 2000). Podle literárních, archeologických i antropologických zdrojů reprezentuje Velká Morava společnost se složitou sociální stratifikací (Stloukal and Vyhnánek, 1976; Havlík, 1978; Poulík, 1985; Velemínský and Poláček, 2008).

Sídlíště Mikulčice bylo situováno v údolí řeky Moravy, jejíž ramena poskytovala přirozenou ochranu centru Mikulčic vybudovanému na písčítých dunách. Opevněné Mikulčice byly důležitou křižovatkou obchodních cest (Květ, 1999), zároveň poskytovaly příznivé životní podmínky pro své obyvatele (Bodri and Čermák, 1995; Poláček, 2008). Nejvyšší koncentrace politické a duchovní moci velkomoravské říše se podle archeologických výzkumů soustřeďovalo právě zde (Poulík, 1975; Klanica, 1985; Poláček, 2008). Během 55 let trvajících archeologického výzkumu bylo v Mikulčické aglomeraci odkryto více než 2500 hrobů, většinou z 9. století (Poláček and Marek, 2005). Tak představují Mikulčice jeden z největších a nejucelenějších populačních vzorků raně středověké Evropy.

Již během prvních terénních výzkumů v padesátých letech 20. století (Poulík, 1975, 1985; Klanica, 1985) byly objeveny sociálně odlišné obydlené regiony Mikulčické aglomerace: opevněný hrad (akropole), částečně opevněné podhradí a venkovské zázemí (Poláček, 2008). Hrad s mnoha kostely, knížecím palácem a řemeslnými dílnami představuje hlavní sídelní a spirituální oblast (Poláček, 2008). V okolí kostelů bylo odhaleno množství pohřebišť, které pravděpodobně reprezentují vyšší socioekonomické třídy obyvatelstva, neboť

kostel a zejména relikvie hrály v raném středověku klíčovou roli (Ohler, 2001; Buko, 2008). Zároveň zde bylo zřejmě pohřbeno mnoho lidí poskytujících služby knížecímu paláci (Poláček, 2008).

Vně souvislého opevnění bylo odkryto další pohřebiště v podhradí. Předpokládá se, že zde byli pohřbeni představitelé středních a nižších tříd (Stloukal and Vyhnánek, 1976; Havlík, 1978; Poláček, 2000, 2008). Kostely v podhradí byly pravděpodobně zakládány vyššími třídami žijícími v blízkosti knížecího paláce, což lze vysvětlit nálezy bohatých hrobů bojovníků (Poláček, 2008). Obyvatelé podhradí se podíleli na fungování hradu a poskytování služeb privilegovaným třídám, žila zde pravděpodobně i vojenská posádka (Klanica, 1987; Staňa, 1997; Poláček and Marek, 2005; Hladík et al., 2008). Zázemí mělo vesnický charakter a výrazně se lišilo od hradu a podhradí. Stále však zůstává otázka, jak výrazné byly socioekonomické rozdíly mezi hradem a podhradím (Poláček, 2008; Macháček, 2010).

Strava obyvatel Mikulčic zahrnovala obiloviny, luštěniny, ořechy a ovoce (Macháček, 2010). Vyšší třídy měly ve stravě větší podíl prosa a masa, nižší třídy se živily zejména obilovinami, což potvrzuje analýza stabilního C, N v kostech (Smrčka et al., 2008), či vyšší výskyt zubního kazu u nižších tříd (Stránská et al., 2008). Jiné skeletální indikátory socioekonomické stratifikace, např. výška postavy (Dobisíková et al., 2008) či hypoplazie zubní skloviny (Trefný and Velemínský, 2008), rozdíly mezi hradem a podhradím neprokázaly.

Co se týká sociálních rozdílů mezi pohlavími (určení pohlaví viz Stloukal, 1963, 1964, 1967, 1969, 1981; Stloukal and Hanáková, 1985; Murail et al., 2005; Velemínský et al., 2005; Brůžek and Velemínský, 2008), je pravděpodobné, že ženy měly nižší pozici než muži. Zubním kazem byly více zasaženy ženy (Stránská et al., 2008). U žen z hradu se vyskytovaly entezopatie v nejvyšší míře (Havelková et al., 2011). I u jiných středověkých společností bylo pozorováno (na základě hypoplazie zubní skloviny, výskytu Harrisových linií, či incidence

zubního kazu) že ženy měly nižší socioekonomickou pozici než muži, snad v souvislosti s rozdílnou dostupností zdrojů potravy (Šlaus, 2000; Esclassan et al., 2009; Lucas et al., 2010). Vysoká variabilita žen zvláště z vyšších tříd je vysvětlována patrilokalitou, zvykovým fenoménem raně středověké populace (Ennen, 2001). Ženy byly přiváděny do manželova domu, ženy vyšších tříd pocházely tedy pravděpodobně ze vzdálenějších komunit než ženy prostšího původu.

1.2.3 Počátek dvacátého století

Třetí soubor je tvořen skelety vzácné Pachnerovy sbírky uložené v osteologickém depozitáři Katedry antropologie a genetiky člověka Přírodovědecké fakulty Univerzity Karlovy. Jedná se o pitevní kolekci pocházející z 30. let 20. století s dobovou dokumentací (jméno, pohlaví, věk, výška postavy, diagnóza). Tato sbírka vznikla pro potřeby profesora Pachnera a Borovanského za účelem sledování pohlavních rozdílů lidské pánve a lebky v letech 1933-39 (Borovanský, 1936; Pachner, 1937).

Podle prof. Pachnera sestává kolekce z městské chudiny Čech, pravděpodobně se jednalo o jedince, kteří neměli rodinu ani prostředky na vypravení pohřbu. Špatnou socioekonomickou situaci a zatížení vysokým stupněm environmentálního stresu těchto lidí podporují také výsledky studií, v nichž byla hodnocena tato sbírka. Direkcionální asymetrie (DA) a fluktuační asymetrie (FA) ve velikosti kostí končetin byla zaznamenána vyšší u Pachnerovy sbírky než u velkomoravské populace, což svědčí o vyšší fyzické námaze, horší stravě a celkově vyššímu stresu recentní sbírky (Kujanová et al., 2008). Pohlavní dimorfismus velikosti u Pachnerovy sbírky je ve srovnání s velkomoravskou populací nižší (Žaloudková, 2004; Fialová, 2004), což opět svědčí o horším zdravotním stavu a vyšší zátěži u recentní sbírky (např. Lazenby, 2001). Dalším indikátorem nedostatečné výživy a horších životních

podmínek Pachnerovy kolekce je gracilita kosterního aparátu (Žaloudková, 2004; Fialová, 2004; Bigoni et al., 2005). Zdravotní stav chrupu a zejména intravitální ztráty zubů také indikují horší zdravotní stav jedinců této kolekce (Stránská et al., 2005).

Kapitola 2

Vlastní práce a výsledky

V této kapitole je detailněji prezentována problematika, cíle a výsledky jednotlivých předkládaných publikací (Bigoni et al., 2005, 2010 a; Kujanová et al., 2008; Velemínská et al., 2008 a, 2012), příspěvků na konferencích (Velemínská et al., 2009; Bigoni et al., 2010 b) a publikace v recenzním řízení (Bigoni et al.).

2.1 Asymetrie

Bilaterální asymetrie, neboli odchylka od perfektní symetrie, patří mezi základní charakteristiky bilaterálních organismů a do určité míry je fyziologická. Tyto, na první pohled nepostihnutelné, jemné asymetrie (do 1% velikosti znaku) odráží schopnost/neschopnost organismu tlumit efekty rozmanitých stresů během vývoje (Palmer, 1994; Palmer and Strobeck, 2003; Schaefer et al., 2006). Kostra uchovává některé znaky vypovídající o zdraví člověka a známky stresu, kterému je během života vystaven. Kosterní asymetrie se zdá být jedním z hlavních ukazatelů tohoto stresu, vývojové stability a nevyrovnané funkční zátěže obou stran těla. Sledováním kosterní asymetrie populací lze tedy porovnávat různé modely

chování, životní podmínky, zdravotní stav, socioekonomické rozdíly a variabilitu uvnitř a mezi sledovanými populacemi (např. Ruff and Jones, 1981; DeLeon, 2007; Schaefer and Bookstein, 2009).

Ve variabilitě bilaterálních znaků v současné době rozlišujeme tři základní typy asymetrie: asymetrii direkcionální, flukтуаční a antisymetrii, vznikající z odlišných příčin (Van Valen, 1962; Palmer and Strobeck, 2003). V naší studii se zabýváme asymetrií direkcionální a flukтуаční, neboť odráží socioekonomickou strukturu sledovaných populací.

Direkcionální asymetrie (DA) je taková bilaterální odchylka v souboru jedinců, kdy jedna strana je konsistentně odlišná od druhé ve tvaru nebo velikosti (Palmer, 1994; Klingenberg et al., 2002). Na lidském skeletu je nejvýraznějším příkladem delší a robustnější pravá horní a levá dolní končetina a to v souvislosti s funkční lateralitou končetin (Schell et al., 1985; Čuk et al., 2001). Pravděpodobně se zakládá brzy v ontogenezi (Pande and Singh, 1971) a dále se rozvíjí nejčastěji v souvislosti s biomechanickými faktory, působícími nesterjně na obě strany těla a to v souvislosti s opakovanými činnostmi a zvykovým chováním člověka (Čuk et al., 2001; Auerbach and Ruff, 2006; Cavalier and Picaud, 2008; Gomes et al., 2011). Příčiny vzniku však mohou mít i genetický podklad (Schultz, 1937; Stirland, 1993). Významným faktorem je environmentální stres (Albert and Greene, 1999; Schaefer et al., 2006), vliv mají zřejmě i ontogenetické faktory spojené s věkem a pohlavím (Helmkamp and Falk, 1990; Stirland, 1993). Vyšší fyzická aktivita zvyšuje DA (Trinkaus et al., 1994; Auerbach and Ruff, 2006).

Flukтуаční asymetrie (FA) představuje nepatrné nepravidelné odchylky mezi korespondujícími částmi pravé a levé strany v souboru, a to bez směru. Je pravděpodobně způsobena nestabilitou během ontogenetického vývoje (vývojovým „šumem“), kterou se snaží tlumit vývojová stabilita (schopnost organismu vytvářet ideální – symetrické formy za daných podmínek) (Zakharov, 1992) a kanalizace (schopnost organismu se vyvíjet podle

ideální vývojové trajektorie za rozmanitých environmentálních podmínek) (Waddington, 1942). FA se může zvyšovat, buď protože vzrůstá vývojový šum, nebo protože klesá vývojová stabilita (Van Valen, 1962; Palmer and Strobeck, 2003). Ačkoliv nelze vymezit relativní příspěvy těchto dvou fenoménů, FA bývá považována za měřítko vývojové stability, zdravotního stavu a zdatnosti organismů a na ně působícího environmentálního stresu (Albert and Greene, 1999; Klingenberg et al., 2002, 2010; Palmer and Strobeck, 2003; Koehler et al., 2004). Environmentální stres (malnutrice, extrémní teploty, hluk, prenatalní chemická léčba, diabetické fetální prostředí, znečištění prostředí, parazitismus, hustota populace) FA zvyšuje (Perzigian, 1977; Parsons, 1990; Zakharov and Graham, 1992; Palmer, 1994; Özener, 2010 b). FA tak odráží životní podmínky a variabilitu populace, souvisí s její socioekonomickou strukturou (Kimmerle and Jantz, 2001; Willmore et al., 2005). FA nemá genetický základ, ovšem některé genetické faktory ji mohou zvyšovat (inbreeding, mutace, apod.) (Livshits and Kobylansky, 1989, 1991; Woolf and Markow, 2003; Schaefer et al., 2006; Özener and Fink, 2010). Pokud se týká intersexuálních rozdílů, některé studie diskutují lepší schopnost tlumit poruchy správného vývoje u žen (Klein, 2004; Møller et al., 2009), a to zejména za nepříznivých podmínek (Özener, 2010 b). Zároveň jsou vyšší hodnoty FA spojovány s rychlou morfologickou změnou uvnitř populace (Kimmerle and Jantz, 2002). FA dosahuje různých hodnot v rozdílných morfologických regionech (DeLeon, 2007; DeLeon and Richtsmeier, 2009).

Antisymetrie, pokud jde o velikostní charakteristiky, má ploché či bimodální rozložení rozdílů pravé a levé strany kolem průměru v nule. Jinými slovy, jedna strana vždy převažuje (jde o signifikantní rozdíly), ale je variabilní, zda je to pravá či levá (Van Valen, 1962).

2.1.1 Velikostní asymetrie kostí končetin

V této části práce jsme se soustředili na asymetrii velikostních charakteristik dlouhých kostí končetin. Výzkum kosterní asymetrie se v odborné literatuře objevuje již v 19. století. Pravděpodobně první prací zabývající se asymetrií na kostech, je studie anatoma Arnolda (1844), který popsal délkovou dominanci pravé pažní kosti a kostí předloktí a zároveň levé kosti stehenní. U člověka se nejvýrazněji kosterní DA projevuje právě na kostech horní končetiny, méně výrazná je na končetině dolní. Některé studie prokázaly, že jistý stupeň asymetrie je ve skutečnosti normou pro délky pažní a stehenní kosti (např. Helmkamp and Falk, 1990). Důvodem většího rozvoje jedné, dominantní horní končetiny je pravděpodobně asymetrické zatížení horních končetin spojené s handedness (preferance jedné horní končetiny; pravorukost a levorukost), zatímco dolní končetiny jsou používány více stejnoměrně, např. při chůzi (Schultz, 1937; Ruff and Jones, 1981; Schell et al., 1985; Stirland, 1993, 1998; Roy et al., 1994; Steele and Mays, 1995; Čuk et al., 2001; Auerbach and Ruff, 2006). Handedness je spojována s asymetrickým vývojem mozku, který odráží dominanci levé mozkové hemisféry (Falk, 1980; White et al., 1994; Annett, 2003).

Většina lidí má více vyvinutou pravou horní končetinu, což souvisí s tím, že většina lidí je pravoruká (přibližně 80-82% jedinců pravorukých, 15% levorukých a 3-5% jedinců bez preference (Steele and Mays, 1995; Mays et al., 1999; Čuk et al., 2001; Annett and Kilshaw, 2011). Nejvíce asymetrickou kostí je humerus. Zápěstí a rameno jsou více asymetricky stresovány než loket (Čuk et al., 2001). Klíční kost bývá na pravé straně kratší, pravděpodobně právě v souvislosti s mohutným rozvojem svalů v tomto místě na úkor jejího růstu (Mays et al., 1999).

Na dolní končetině je DA méně častá a výrazná, zřejmě v souvislosti s více symetrickou zátěží např. při lokomoci (Ruff and Jones, 1981; Macho, 1991; Čuk et al., 2001; Auerbach and Ruff, 2006). Studium asymetrie dolní končetiny většinou ukazuje na více

vyvinutou levou dolní končetinu a to bez ohledu na handedness, levá končetina má opěrnou nosnou funkci, což je vyjádřeno délkou femuru (Macho, 1991; Čuk et al., 2001; Plochocki, 2004). Tibie oproti tomu projevuje zkříženou asymetrii, tedy delší pravá horní končetina – delší levá tibie a naopak (Čuk et al., 2001). Pravá dolní končetina je používána ke specifitějším úkonům (např. kopání), zátěž je kladena zejména na koleno, proto se DA projevuje u některých rozměrů epifyzárních částí ve prospěch pravé strany (Plato et al., 1985; Macho, 1991; Čuk et al., 2001; Singh and Mohanty, 2005). Pravá dolní končetina je dominantní, většina lidí je pravonohá. U dolních končetin byl zaznamenán nižší výskyt DA u délek a epifyzárních částí kostí než u diafyzárních částí kostí, což bývá spojováno s tím, že tělo kosti více podléhá vlivů různých environmentálních faktorů než délka a epifyzární části kosti (Ruff and Jones, 1981; Lieberman et al., 2001; Ruff, 2003; Auerbach and Ruff, 2006). Tuto skutečnost lze také spojovat s tím, že růst kosti do délky je ukončen mezi 18. a 25. rokem života zatímco do šířky růst pokračuje během celého života (Čuk et al., 2001; Ahlborg et al., 2003; Lazenby, 2005).

Podle Čuk et al. (2001) odráží stupeň DA stupeň zátěže kladený na danou končetinu, lokalizace DA pak indikuje druh užití síly. Lokalizace a stupeň DA kostí končetin tak souvisí se specifickými aktivitami odrážejícími subsistenční adaptaci a socioekonomickou strukturu dané populace včetně rozdílů mezi populacemi a intersexuálních rozdílů a to jak u délkošířkových rozměrů, tak také u geometrie průřezů dlouhých kostí (Ruff and Jones, 1981; Fresia et al., 1990; Trinkaus et al., 1994; Bridges, 1995; Bridges et al., 2000; Stock and Pfeiffer, 2001; Weiss, 2003, 2005, 2009; Auerbach and Ruff, 2006; Sládek et al., 2006 a; b, 2007; Sparacello and Marchi, 2008; Maggiano et al., 2008; Özener, 2010 a; Sparacello et al., 2011). Podle některých studií však nemusí délkové a epifyzární rozměry odrážet míru mechanické zátěže, ale spíše působení dalších genetických či environmentálních faktorů (Trinkaus et al., 1994; Lieberman et al., 2001; Ruff, 2003; Sládek et al., 2007).

Jak bylo popsáno výše, na bilaterální asymetrii končetin se podílí zejména biomechanické faktory, avšak významnou úlohu hrají také faktory environmentální. Stresy genetického a environmentálního původu zvyšují hodnoty FA končetin (Schell et al., 1985; Graham et al., 1993; Markow, 1994; Albert and Greene, 1999; Polak, 2003). FA se však na kostech končetin (zejména horních) projevuje méně než DA, neboť asymetrické mechanické zatížení končetin je značné. Navíc vývojová stabilita je pro různé znaky specifická, a to v souvislosti s významností funkce daného znaku. Přírodní výběr tak redukuje FA u znaků, které jsou důležité pro zdatnost organismu (Palmer and Strobeck, 1986). Proto jsou znaky spojené s lokomocí více symetrické než znaky bez spojení s lokomocí (Gummer and Brigham, 1995; Trivers et al., 1999; Debat et al., 2000).

V publikaci **Bigoni et al. (2005)** jsme se soustředili na asymetrii (direkcionální, flukтуаční, popř. zkříženou) horní a dolní končetiny identifikované Pachnerovy sbírky (celkem 143 mužských a 157 ženských skeletů) (Borovanský, 1936; Pachner, 1937). Hodnotili jsme ji na základě metrických parametrů kosti pažní, loketní, vřetenní, klíční, lopatky (celkem 21 rozměrů) a kosti stehenní, lýtkové a holenní (27 rozměrů). Přítomnost antisymetrie byla vyloučena graficky. Přítomnost a hodnota DA byla testována párovým t-testem (Palmer, 1994), velikost FA byla hodnocena pomocí vzorců z publikace Palmer and Strobeck (1986). Zkřížená asymetrie byla sledována na základě maximálních délek kosti pažní vs. kosti stehenní, lýtkové a holenní (Steele and Mays, 1995; Čuk et al., 2001).

Dospěli jsme k následujícím závěrům:

- Antisymetrie nebyla zaznamenána u žádného sledovaného rozměru

- Přítomnost DA byla častěji zaznamenána u horní končetiny, u dolní byla častější FA. Vysvětlením je zřejmě více asymetrické používání horní končetiny oproti symetrickému využití dolní končetiny zejména při chůzi
- Nejvíce asymetrickou kostí byla kost pažní, pravděpodobně odrážející funkční preferenci ruky, s dominancí pravé strany. Rozdělení souboru podle délky pažní kosti odpovídalo procentuálnímu zastoupení pravorukých a levorukých jedinců v současné populaci
- Kostí předloktí také projevovaly DA ve prospěch pravé strany. Pravděpodobně je tedy kosterní asymetrie resistantní vůči kulturním tlakům na „přepínání“ handedness v souvislosti s tím, že se tendence pro používání výhradně pravé ruky ke psaní na kostře neodráží, neboť při tomto úkonu není mechanická zátěž tak významná, na rozdíl od jiných aktivit, kdy je ponechána volnost ve volbě dominantní končetiny
- Na dolní končetině byla zaznamenána DA pouze na stehenní kosti a to většinou ve prospěch levé strany a častěji u žen
- Zkřížená asymetrie kost pažní-kost holenní byla pozorována pouze u mužů, oporná funkce levé dolní končetiny bez ohledu na handedness byla vyjádřena levostrannou DA stehenní kosti

V předkládané publikaci **Kujanová et al. (2008)** jsme zpracovávali dva časově vzdálené soubory kosterních pozůstatků dospělé střeoevropské populace z téže geografické oblasti s předpokládanou nestejnou environmentální zátěží. Tento předpoklad jsme testovali právě na základě sledování různého výskytu DA a FA kostí končetin u těchto souborů a to s ohledem na pohlaví. První sledovanou sbírkou byla raně středověká populace ze slovanských pohřebišť Mikulčice-Kostelisko (78 mužských a 132 ženských koster) a

Prušánky (66 mužských a 69 ženských koster) datovaných do 9. - 12. století (Poláček and Marek, 2005; Velemínský et al., 2005; Klanica, 2006; Velemínský and Poláček, 2008). Druhou sbírkou byla kolekce identifikovaných postkraniálních skeletů zvaná Pachnerova sbírka (143 mužských a 127 ženských koster). Tato pitevní kolekce pochází z 30. let 20. století a představuje obyvatele Čech z nejnižších sociálních vrstev (Borovanský, 1936; Pachner, 1937).

V této studii jsme analyzovali asymetrii kostí horní končetiny (kosti pažní, loketní a vřetenní, lopatky a kosti klíční) a kostí dolní končetiny (kosti stehenní, holenní a lýtkové) a to pouze v případě zachovaných měřitelných charakteristik na obou párových kostech. Přítomnost a stupeň DA byla testována párovým t-testem (Palmer, 1994). V případě nepřítomnosti DA ani antisymetrie (grafické ověření normální distribuce znaku) byla sledována přítomnost a hodnota FA pomocí vzorců z publikace Palmer and Strobeck (1986). Rozdíly distribuce asymetrie mezi sledovanými soubory byl testován pomocí dvouvýběrového neparametrického Mann-Whitneova U-testu.

V předkládané studii Kujanová et al. (2008) jsme dospěli k následujícím závěrům:

- DA byla zaznamenána u většiny dimenzí kostí horní končetiny a, s výjimkou délky kosti klíční, směřovala DA vždy doprava. Důvodem je výrazně asymetrické používání horní končetiny k různým manipulativním úkonům, přičemž užívání horní končetiny odpovídá stranové preferenci v souvislosti s handedness (až 85% populace je pravorukých)
- Méně často a méně výrazná byla DA pozorována u rozměrů kostí končetiny dolní a, s výjimkou šířky horní epifyzární části kosti stehenní, směřovala vždy doleva. Důvodem je více symetrická zátěž dolní končetiny např. při chůzi. Levá dolní

končetina má opěrnou funkci, pravá dolní končetina je dominantní pro více specifické úkony, jako je kopání, což je vyjádřeno právě pravostrannou DA epifyzárních částí

- Interpopulační srovnání výskytu a stupně DA ukázalo, že častěji a výrazněji se DA projevila u vzorku recentní populace. Důvodem je blíže nespecifický vývojový stres předpokládané městské chudiny, snad v souvislosti s vyšší mechanickou zátěží při těžké práci a výrazným nutričním a jiným environmentálním stresem
- FA dosahovala na kostech horní a dolní končetiny nízkých až zanedbatelných hodnot, což vypovídá zejména o vysokém výskytu DA u sledovaných rozměrů. Nejvyšší hodnoty byly pozorovány u kosti klíční, lopatky a u některých rozměrů kosti holenní
- Vyšších hodnot dosahovala FA u recentní populace, což podporuje předpoklad, že populace z Mikulčic jako celek existovala v příznivých životních podmínkách, zatímco Pachnerova kolekce představuje vysoce environmentálně stresovaný vzorek recentní populace. Porovnáváme-li muže a ženy odděleně, FA mužů je výraznější u recentní sbírky, ale u žen je situace obou souborů podobná, což by mohlo souviset s rozdílným socioekonomickým postavením žen a mužů ve středověku
- Hodnocení kosterní bilaterální asymetrie minulých populací je významným ukazatelem jejich životního stylu, prostředí, mechanického a environmentálního stresu a socioekonomických rozdílů mezi zkoumanými populacemi. Je významnou součástí hodnocení skeletální variability na daném území

2.1.2 Tvarová asymetrie lebky

Tato kapitola je věnována tvarové asymetrii lebky. Asymetrie tvaru lebky jako celku představuje odchylku od symetrie objektu, kdy je daná struktura bilaterálně symetrická, takže její levá a pravá polovina jsou vzájemnými zrcadlovými obrazy (Mardia et al., 2000; Klingenberg et al., 2002). Na lebce je nejvýraznější asymetrie většinou spojena s určitou patologií, jako jsou třeba rozštěpy rtu a patra nebo kraniosynostózy (Bock and Bowman, 2005; Netherway et al., 2006). Existují další znaky DA, kdy je kraniofaciální změna tvaru sekundárním následkem konkrétního onemocnění, např. autismu (Hammond et al., 2008). Zároveň však jsou jemné kraniofaciální asymetrie běžné u zdravé populace (DeLeon, 2007; Ercan et al., 2008).

Faciální DA je výrazně ovlivněna biomechanickou námahou při žvýkací funkci, která je spojována se subsistenční adaptací a přidruženým chováním (Vig and Hewitt, 1975; Carlson and Van Gerven, 1977; Ferrario et al., 1997; Moreira et al., 2008; Gomes et al., 2011). Žvýkací návyk je spojen se stravou a strava minulých populací může být použita pro odhad jejich sociální stratifikace (Le Huray and Schutkowski, 2005). Nejvíce se žvýkací návyk projevuje v asymetrickém růstu horní a dolní čelisti a lícnicích kostí. Žvýkací návyk je asymetrický, většina populace preferuje ke žvýkání pravou stranu úst (Nissan et al., 2004; Diernberger et al., 2008; Martinez-Gomis et al., 2009). Kraniofaciální DA se ale neobjevuje až s ustavením žvýkacího návyku, nýbrž je pozorována již brzy během života plodu a zůstává na stejném stupni během dalšího vývoje jedince (Rossi et al., 2003; Moreira et al., 2008). Některé předchozí studie popisují levou stranu obličeje jako dominantní (Woo, 1931; Vig and Hewitt, 1975; McIntyre and Mossey, 2002; Ercan et al., 2008), jiné naopak dominanci pravé strany (Farkas and Cheung, 1981; Ferrario et al., 1994, 1995; Shaner et al., 2000). Podle Ercan et al. (2008) vzniká tento rozpor použitím různých metod. Očnice rotují ve stejném

směru jako klenba lební, ale jejich dolní okraj reaguje na zátěž podobně jako horní čelist a lícní kosti (Ercan et al., 2008).

Klenba lební při osifikaci následuje asymetrický růst mozku, který je také závislý na stravě jedince (Menegaz et al., 2010; Cray Jr. et al., 2011). Asymetrie mozku se začíná vyvíjet prenatálně, levá hemisféra kontroluje pravou ruku, která je u většiny populace dominantní (Annett, 2003; Sun and Walsh, 2006). Pravá hemisféra je specializována na prostorové vnímání, levá je dominantní pro logické myšlení a jazyk (Riss, 1984; Geschwind and Miller, 2001). V předchozích studiích je většinou popisována pravá hemisféra větší v horní a zadní části, ale menší v basikraniálním regionu (Woo, 1931; Hershkovitz et al., 1992; Rossi et al., 2003), a tento fenomén je stabilní v různých populacích, podobně jako handedness.

Výrazné asymetrie lebky vznikají deformačně v souvislosti s polohováním dětí na zádech jako prevenci syndromu náhlého úmrtí kojence (Chan et al., 1995; Dias a Klein, 1996; Turk et al., 1996; Martínez-Lage et al., 2006; Cavalier a Picaud, 2008). Přesto tento jev není dostatečným vysvětlením vzrůstajícího výskytu deformační plagiocefalie v této době (Dias and Klein, 1996). Tyto deformace mohou být bez včasné léčby trvalé (Chan et al., 1995). Je tedy možné, že i jemné asymetrie lebky v našem souboru souvisí se zvykovým chováním populace, jako je polohování, houpání nebo nošení dětí v šátku (Manning and Chamberlain, 1991; Kohn et al., 1995; Manning et al., 1997; Bourne and Todd, 2004).

Ačkoliv baze, klenba a obličej pochází z embryologicky rozdílných regionů, vytváří společně jeden komplexní celek s mnoha vývojovými a funkčními interakcemi (Cheverud, 1982; Enlow, 1990; Lieberman et al., 2000). Baze se vyvíjí více symetricky než ostatní části lebky, pravděpodobně proto, že její osifikace je na rozdíl od ostatních regionů enchondrální a začíná již brzy během života plodu (Enlow, 1990; Carlson, 1999; Macaluso, 2012). Celkově je tvar a velikost baze do značné míry nezávislý na ostatních strukturách lebky (Lieberman et al., 2000). Kwon et al. (2006) popsal, že stupeň DA lebeční baze se neliší mezi populačními

vzorky s a bez faciální asymetrie. Kohn et al (1995) popisují, že cradleboarding nemá dopad na morfologii lebeční baze. Je možné, že různé životní podmínky a každodenní zvykové aktivity nezanechávají stopy na tomto morfologickém regionu.

FA lebky v souvislosti s různými genetickými a environmentálními stresy bývá studována zejména na tvaru a velikosti zubního oblouku (Niswander and Chung, 1965; Bailit et al., 1970; Doyle and Johnston, 1977; Bishara et al., 1994; Schaefer et al., 2006). Vyšší dentální asymetrie je indikátorem environmentálního stresu, škodlivých vnějších podmínek, genetických faktorů a celkového zdravotního stavu populace (Siegel and Doyle, 1975; Doyle and Johnston, 1977; Kieser et al., 1986; Kimmerle and Jantz, 2001; Schaefer et al., 2006). Proto mnoho studií využívá dentální FA právě jako nepřímé měřítko těchto stresů různých historických i současných populací (Townsend and Brown, 1980; Townsend, 1981; Sharma et al., 1986; Hershkovitz et al., 1987, 2005; Barden, 2005; Dibennardo and Bailit, 2005; Harris and Nweeia, 2005; Schaefer et al., 2006).

Kraniofaciální FA je spojována s mužskou a ženskou genotypovou a fenotypovou kvalitou (Gangestad and Scheyd, 2005; Özener and Fink, 2010; Özener, 2010 b). Existuje také spojení obličejové symetrie a atraktivity jedince pro opačné pohlaví, avšak hodnotící jedinec není schopen odhalit faciální asymetrie přesně (Thornhill and Gangestad, 1994, 1999; Scheib et al., 1999). Zároveň jsou k posouzení fenotypové kondice jedince používány jiné znaky atraktivity (Scheib et al., 1999).

FA dosahuje různých hodnot v různých morfologických regionech, vývojová nestabilita je znakově specifická (DeLeon, 2007). Nejnížší hodnoty byly popsány v mediální rovině, což souvisí s jejich větší funkční důležitostí než u laterálních bodů např. na klenbě lebeční. Změna polohy některých struktur či oblastí lebky by měla výrazný dopad na další struktury, se kterými jsou funkčně spojeny. Zde by i jen malá odchylka mohla narušit funkci (např. otvory, kanálky). U jiných bodů (např. v oblasti klenby lebeční) nehraje jejich jemný

posun tak významnou roli, nadále plní svou funkci. Jde o tzv. hypotézu funkcionality (Gummer and Brigham, 1995; Trivers et al., 1999; DeLeon, 2007). Nižších hodnot dosahuje FA také v oblasti obličeje (DeLeon, 2007). Vysvětlení je kladeno do roviny signalizace reprodukční zdatnosti, pohlavního výběru a atraktivity, kdy zde přírodní výběr musí nutně snižovat FA, neboť je obličej příliš viditelný (Thornhill and Gangestad, 1994, 1996; Swaddle, 1998). Jde o tzv. hypotézu signalizační (Uetz and Taylor, 2003; DeLeon, 2007). Tato teorie může vysvětlovat i již popisovanou nižší FA u mediálních bodů, které jsou také více viditelné než ty laterální na klenbě. Zároveň by tato teorie vysvětlovala zjištěnou větší FA na bazi, kde byla nižší FA předpokladem vysoké důležitosti a malé variability. Opět to pravděpodobně souvisí s tím, že baze není vidět a neplní signalizační funkci, která je pro lebeční FA rozhodující.

Na tentýž environmentální stres reagují ženy a muži odlišně, ale předmětem diskuze nadále zůstává, jak odlišit vliv environmentálních a biologických faktorů (Özener, 2010 b). V horších environmentálních podmínkách nižších socioekonomických skupin se projevuje lepší schopnost tlumit negativní vlivy prostředí u žen, u vyšších sociálních vrstev však rozdíly zaznamenány nebyly (Özener, 2010 b).

Odhad rozdílného stupně environmentálního stresu pomocí geometricko-morfometrického stanovení kraniofaciální FA bylo v předchozích studiích využito např. mezi lidmi s různým socioekonomickým postavením v Turecku (Özener, 2010 b), mezi jedinci z raně a pozdně křesťanských hřbitovů v Nubii (DeLeon, 2007), nebo mezi inbredním a outbredním souborem adriatické populace (Schaefer et al., 2006). Při porovnání středověkých a moderních lebek, Gawlikowska et al. (2007) popisují vyšší hodnoty FA u moderního souboru. Autoři vidí příčinu ve výraznějším vlivu vývojového stresu a slabší schopnosti jej kompenzovat (Gawlikowska-Sroka, 2006; Gawlikowska et al., 2007).

V předkládané publikaci **Bigoni et al. (v recenzním řízení)** jsme se snažili odpovědět na otázku socioekonomické struktury raně středověké společnosti sídliště v Mikulčicích a to pomocí stanovení kraniofaciální DA a FA s ohledem na pohlaví. Soustředili jsme se na rozdíly v lokalizaci a stupni asymetrie mezi soubory lebek pocházejících z předpokládaných různě socioekonomicky postavených obydlených částí Mikulčického sídliště. Prvním souborem je 129 lebek (61 ženských a 68 mužských) z Mikulčického hradu, tzn. z pohřebišť v okolí I., II., III., IV., a XI. kostela, z předpokládaných vyšších socioekonomických tříd. Druhým souborem je 71 lebek (38 ženských a 33 mužských) z Mikulčického podhradí, konkrétně z pohřebišť z Kosteliska, Klášteřiska a v okolí IX. kostela, z předpokládaných středních a nižších tříd. Jako srovnávací soubor je použito 138 lebek (65 ženských a 73 mužských) známého pohlaví Pachnerovy sbírky, z předpokládaných nejnižších socioekonomických tříd české populace přelomu 19. a 20. století.

V této studii jsme analyzovali tvarovou asymetrii lebky pomocí metod geometrické morfometrie. Celkem byly pomocí MicroScribe G2X digitalizovány 3D koordináty 68 ektokraniálních landmarků (10 nepárových a 29 párových). Na základě předpokládaného rozdílného stupně DA a FA byly landmarky rozděleny do tří regionů – horní obličej (29 landmarků), oblast klenby (24 landmarků) a lebeční baze (23 landmarků).

Po Procrustovské analýze byl zrcadlením původního objektu vytvořen jeho zrcadlový obraz („reabeled reflection“), jejich průměrem je absolutně symetrický tvar. Individuální asymetrie jednotlivých lebek byla spočítána jako rozdíl zrcadleného obrazu a původního objektu. DA byla vypočtena jako průměr individuálních asymetrií ve vzorku. Pro každého jedince byla poté spočítána FA jako rozdíl individuální a direkcionální asymetrie. Díky tomuto postupu nebylo nutné definovat mediální rovinu a bylo možné studovat asymetrický posun i landmarků snímaných v hypotetické mediální rovině. Statistická významnost rozdílů individuální asymetrie mezi skupinami byla počítána pomocí Hotellingova T^2 testu s

permutací. Statistická významnost velikosti DA ve vzorku byla ověřena pomocí Procrustes ANOVA, což je MANOVA pro neizotropní data. Sumarizované vektory FA byly statisticky testovány mezi soubory pomocí ANOVA.

V předkládané studii Bigoni et al. (v recenzním řízení) jsme dospěli k následujícím závěrům:

- Odhad kraniofaciální asymetrie potvrdilo socioekonomické rozdíly mezi hradem a podhradím Mikulčického sídliště. Rozdíly jsou výraznější u žen než u mužů
- Soubory z Mikulčic se lišily ve stupni DA, ne však v jejím směru. Směr DA u očnic, klenby a lebeční baze byl podobný u souborů z Mikulčic i Pachnerovy kolekce. Okraje očnic rotovaly proti směru hodinových ručiček, pravá očnice byla relativně nižší a širší, levá více oválná. Pravá polovina klenby byla relativně širší a vyšší. Její spodní část však byla relativně širší na levé straně, podobně jako lebeční baze. Landmarky blízko mediánní roviny, horní čelist a lící kosti vykazovaly opačný směr u Mikulčických souborů než u Pachnerovy kolekce. Mediánní landmarky souborů z Mikulčic rotovaly ve směru hodinových ručiček, pravá strana horního obličeje se relativně zužovala v pravolevém směru. Levá strana obličeje byla širší ale nižší než pravá. Lící oblouk byl na pravé straně relativně vyšší. Tyto změny měly opačný směr u Pachnerovy sbírky
- Obyvatelé Mikulčic, dokonce i ti považovaní za nižší sociální skupiny, žili v příznivých životních podmínkách a požívali tužší stravu než jedinci Pachnerovy sbírky. FA i DA ukazují na výrazné socioekonomické rozdíly mezi Pachnerovou sbírkou a populací z Mikulčic a to ve prospěch Mikulčic
- Rozdílná strava mezi různými socioekonomickými skupinami v Mikulčicích byla potvrzena pomocí DA horního obličeje a klenby, kde byly zaznamenány největší

rozdíly mezi skupinami. Obyvatelé Mikulčického podhradí byli vystaveni nesignifikantně větším hodnotám biomechanického stresu ovlivňujícím horní obličej a klenbu lebeční. Důvodem je pravděpodobně hrubší a tužší strava podhradí, jako jsou obilniny, oproti většímu podílu masa ve výživě obyvatel hradu. Nejnižších hodnot dosahovala DA horního obličeje u Pachnerovy sbírky, zřejmě v souvislosti s předpokládanou více tekutou stravou a celkově nedostatečnou výživou

- Intersexuální rozdíly byly pozorovány v asymetrii tvaru klenby, podobně jako za použití velikostních charakteristik lebky. Zatímco muži z hradu a podhradí jsou si vzájemně více podobní, u žen existují větší rozdíly. Ženy Mikulčického podhradí byly menší a zároveň více direkcionálně asymetrické v oblasti klenby než ženy z hradu. To podporuje hypotézu, že muži pohřbení na hradě a podhradí v Mikulčicích pocházeli z vyšších stejně jako ze středních a nižších vrstev obyvatelstva. Naopak, ženy z podhradí pravděpodobně pocházely z nižších socioekonomických skupin než ženy pohřbené na hradě.
- U mužů nebyly zaznamenány rozdíly v FA mezi hradem a podhradím z Mikulčic. U žen naopak byly rozdíly ve stupni FA signifikantní, ženy z hradu překvapivě dosahovaly vyšších hodnot. FA žen z hradu byla podobná jako FA vysoce stresované Pachnerovy kolekce. Předpokládáme, i s ohledem na výsledky DA, že důvodem může být větší variabilita žen z hradu v porovnání s ostatními skupinami z Mikulčic a to díky raně středověkému fenoménu – patrilokalitě. Ženy hradu pravděpodobně pocházely ze vzdálenějších sídlišť než ženy podobně přivdané do podhradí

2.2 Pohlavní dimorfismus

Mezi další znaky charakterizující variabilitu člověka patří pohlavní dimorfismus, který je výsledkem pohlavního výběru nebo jiných genetických a strukturálních vlivů či vlivu chování člověka (Slatkin, 1984; Lieberman, 2011). Pohlavní dimorfismus člověka je výsledkem rozdílných reprodukčních rolí muže a ženy a silného selekčního tlaku působícího na člověka během evoluce. Stupeň pohlavního dimorfismu je ovlivněn environmentálními faktory a liší se tedy u různých populací. Přesto lze říci, že obecně jsou muži větší, mají robustnější skelet a klouby a silnější muskulaturu než ženy (Baab et al., 2010). Větší velikostní charakteristiky samců jsou typické pro mnoho primátů (Wood, 2006).

2.2.1 Pohlavní dimorfismus lebky a určení pohlaví

Pohlavní dimorfismus na kostře je základem k určení pohlaví u neznámých lidských pozůstatků, a to jak ve forenzních vědách, tak i v archeologii (Graham, 2006; Brinkmann, 2007; Cattaneo, 2007). Ačkoliv je pohlavní diagnóza nejpřesnější a nejspolehlivější použijeme-li pánev (Brůžek and Murail, 2006), její špatná zachovalost může vyžadovat určení pohlaví podle lebky či jiných částí skeletu.

Klasické vizuální metody u lebky dosahují přesnosti určení pohlaví až v 80% (Williams and Rogers, 2006), s využitím diskriminační analýzy až 88% (Walker, 2008). Tento přístup však vykazuje vysokou míru subjektivity a zároveň může být ovlivněn stupněm rozvoje znaku v dané populaci. Výhodou tradičních morfometrických metod je jejich objektivita, nevýhodou populační specifita. Při použití diskriminačních funkcí lebky lze dosáhnout až 85% - 95% přesnosti (Howells, 1965; Steyn and İşcan, 1998; Franklin et al., 2006 a), velikostní pohlavní dimorfismus však u lebky vykazuje významnou interpopulační variabilitu (Kemkes and Göbel, 2006; Rösing et al., 2007; Spradley et al., 2008), která

způsobuje snížení spolehlivosti. Vliv mají demografické změny složení populace i sekulární trend (Susanne et al., 1988; Jantz, 2001; Buretić-Tomljanović et al., 2006; Jonke et al., 2007), nebyl zaznamenán signifikantní vliv věku dospělých jedinců na pohlavní dimorfismus lebky (Nikita, 2012). Přínosem geometrické morfometrie je mimo jiné eliminace subjektivity při hodnocení tvaru, možnost návrhu objektivních kategorií pro nemetrické pohlavně dimorfní znaky a možnost využití semi-landmarků při hodnocení křivek (Franklin et al., 2006 a, 2007, 2012; Perez et al., 2006; Pretorius et al., 2006; Bilfeld et al., 2012).

Ačkoliv jednotlivé části lebky pochází embryologicky z různých regionů, vyvíjí se jako komplexní struktura (Cheverud, 1982; Enlow, 1990; Carlson, 1999; Hennessy et al., 2005; Stynder et al., 2007) skládající se z mnoha morfogenetických (např. neurálních) a funkčních (např. žvýkání, respirace) interakcí (Lieberman et al., 2000; Lieberman, 2011). Tvar lebky, zejména její obličejové části, je nejvýraznější komponentou variability uvnitř a mezi populacemi, jak ukázalo mnoho studií využívajících 3D metody (Hennessy and Stringer, 2002; Bruner and Manzi, 2004; Badawi-Fayad and Cabanis, 2007; Franklin et al., 2007).

Pohlavní dimorfismus lebky je spojen i s fyzickou konstitucí a energetickými požadavky, což lze sledovat zejména v místech úponu svalů (Rosas and Bastir, 2002). Příkladem je faciální prognácie, relativní bizygomatická šíře, stupeň vývoje glabelly a bradavčitých výběžků, profil čela a okcipitální oblasti (Hennessy et al., 2002; Franklin et al., 2006 a). Právě relativní bizygomatická šířka podle autorů determinuje pohlavní rozdíly nejlépe. Popisována bývá oválnější očníce u žen a hranatější (relativně širší a nižší) očníce mužů (Pretorius et al., 2006), zároveň však existují rozdíly i ve vzájemné poloze očnic. Tvar oblasti očnic překvapivě dobře determinuje pohlaví (73-80%) (Pretorius et al., 2006). Více prominující nosní kůstky spolu s hlubší depresí nasionu jsou typické u mužů (Franklin et al., 2006 a), muži mají navíc relativně užší a delší oblast *apertura piriformis*. Oblast patra je u mužů relativně kratší, hlubší a užší než u žen (Šmahel et al., 1998; Franklin et al., 2006 a).

Signifikantní pohlavní dimorfismus velikosti a tvaru bývá popisován také v oblasti baze lební (Holland, 2005; Franklin et al., 2006 a; Bruner and Ripani, 2008; Gapert et al., 2008; Macaluso, 2012). Ve tvaru neurokrania jako celku nebyly popsány významné pohlavní rozdíly, výjimku tvoří tvar mediánní křivky (Šmahel et al., 1998; Franklin et al., 2006 a). Pro ženy je typické kulatější neurokranium, méně prominující glabella a oblast inionu, klenuté čelo, a celkové relativně nižší kranium v oblasti bregmy.

Ve studii **Bigoni et al (2010)** bylo naším cílem analyzovat pohlavní dimorfismus lebky identifikované středoevropské série (Pachnerova sbírka; 73 mužských a 66 ženských dospělých lebek) a ověřit použitelnost tvaru lebky a metod geometrické morfometrie k určení pohlaví. Dalším úkolem bylo lokalizovat oblasti lebky s nejvýraznějším tvarovým pohlavním dimorfismem.

Pohlavní dimorfismus tvaru lebky jsme analyzovali pomocí metod geometrické morfometrie. Pomocí MicroScribe G2X byly digitalizovány 3D koordináty 82 ektokraniálních landmarků (oblast neurokrania, baze lební, horního obličeje, region očnice, nosu a patra). Zároveň bylo nasnímáno 39 semi-landmarků podél mediánní křivky od bodu nasion po opistion. Generalizovaná Prokrustovská analýza (GPA) byla použita pro eliminaci netvarové variability. Signifikance pohlavních rozdílů byla testována pomocí MANOVA. Průměrný tvar a variabilita souboru byla analyzována pomocí PCA (Franklin et al., 2006 a), tvarové rozdíly mezi pohlavími byly vizualizovány pomocí drátového modelu a TPS (thin-plate spline) (Slice, 2007). Pro stanovení přesnosti pohlavní klasifikace byla použita diskriminační analýza (Franklin et al., 2006 b).

Dospěli jsme k následujícím závěrům:

- Pohlavní rozdíly nebyly zaznamenány na lebce jako celku, na lebeční bazi a celkovém tvaru neurokrania
- Signifikantní pohlavní dimorfismus byl zaznamenán v oblastech mediánní křivky, horního obličej, regionu očnice, nosního otvoru a patra
- V oblasti horního obličej byly pohlavní rozdíly nejvýraznější (100% správnost určení pohlaví), muži měli relativně nižší a širší obličej, který byl zároveň plošší a více kolmo postavený. Nejvýraznější pohlavní rozdíly byly zaznamenány na jařmových obloucích, které byly u mužů širší a vyšší než u žen
- Analýza tvaru mediánní křivky (99% správně určeno) ukázala, že ženy mají kulatější neurokranium, zaoblenější čelo bez výrazné glabelly, plošší oblast bregmy a oblý okcipitální region
- Ženy mají oválnější očnice (74% správně určeno) ve srovnání s nižšími a širšími očnicemi mužů. Významná je změna v poloze očnic - okraj očnice je u mužů rovnoběžný s rovinou čela, u žen je položen více v sagitálním směru
- Oblast nosního otvoru (77% správně určeno) je u mužů relativně vyšší a užší s hlubší bází nosu a s více prominujícími nosními kůstkami
- Oblast patra (70% správně určeno) je u žen relativně nižší a širší, u mužů kratší, hlubší a užší
- Analýza tvaru metodami geometrické morfometrie odhalila některé dílčí pohlavní rozdíly, které je obtížné detekovat metricky, a jsou příliš subjektivní při visuálním hodnocení, jako je nestejná orientace očnic či celkový tvar mediánní křivky

2.2.2 Pohlavní dimorfismus obličeje, vztah tvaru a velikosti

Obličej je hlavním rozpoznávacím znakem člověka, odráží jeho identitu (Fanghänel et al., 2006; Blažek and Trnka, 2009). Poskytuje pozorovateli informaci o pohlaví, věku či zdravotním a emocionálním stavu sledovaného jedince (Gangestad and Scheyd, 2005; Thornhill and Gangestad, 2006). Struktura, tvar a velikost obličeje a vzájemná poloha jednotlivých jeho částí je dána zejména geneticky, ale důležitou roli v rámci variability obličeje hrají také environmentální a jiné exogenní faktory (Wood and Lieberman, 2001; González-José et al., 2005; Stynder et al., 2007). Právě na obličejí se výrazně projevují pohlavní rozdíly (Martínez-Abadías et al., 2006).

Pohlavní dimorfismus obličeje je přítomen již v raném prenatálním období, a to vlivem vlastního chromozomálního pohlaví (Fink et al., 2005) a zároveň vlivem hormonální prostředí (vysoká koncentrace fetálního testosteronu či estrogenu) ovlivňujícím robusticitu obličeje plodu (Lutchmaya et al., 2004). Plně se však pohlavní dimorfismus obličeje rozvíjí vlivem odlišné mužské a ženské růstové trajektorie během puberty a dospívání (Ursi et al., 1993; Rosas and Bastir, 2002; Bulygina et al., 2006; Enlow and Hans, 2008). Zejména vlivem výrazného působení testosteronu na rozvoj obličejových znaků, byl zaznamenán signifikantní pohlavní dimorfismus velikostních charakteristik u většiny věkových skupin, a to ve prospěch mužů (Ursi et al., 1993; Ferrario et al., 1998). Jiní autoři zaznamenali intersexuální rozdíly obličejových charakteristik až přibližně od 13. roku, kdy pubertální růst obličeje u dívek končí, ale u chlapců pokračuje (Bishara et al., 1984; Enlow, 1990; Genecov et al., 1990; Farkas and Posnick, 1992).

Vyšší míra testosteronu způsobuje celkové prodloužení obličeje, relativně menší oči a větší nos, laterální růst lících kostí, dolní čelisti a brady, anteriorní růst nadočnicových oblouků a glabelly a prodlužování dolního obličeje. Celkově je mužský obličej robustnější.

Vliv estrogenu vede ke gracilnějšímu oválnějšímu obličejí s drobnějším nosem, bradou a plnějšími rty u žen (Farkas, 1981; Ferrario et al., 1998; Enlow and Hans, 2008; Toma et al., 2008; Schaefer and Bookstein, 2009; Weisensee and Jantz, 2011). Jedním z nejvýznamnějších pohlavně dimorfních znaků obličejí je velikost a stavba nosu a nosohltanu, který ovlivňuje další struktury obličejí (Enlow and Hans, 2008). Důvodem je vyšší energetický požadavek na přísun vzduchu u mužů (Rosas and Bastir, 2002).

V naší studii jsme se soustředili na odlišení velikostních a tvarových pohlavních rozdílů a na jejich vzájemný vztah. V dospělosti jsou významnější intersexuální rozdíly ve velikosti než ve tvaru obličejí (Ferrario et al., 1998, 2000), u většiny lineárních charakteristik dosahují 5 - 10% celkové velikosti znaku (Ferrario et al., 1993; Šmahel et al., 1998). Pokud jde o velikostní charakteristiky obličejí, dospělý mužský obličej je obecně větší, což bylo mnohokrát popsáno v literatuře (Borovanský, 1936; Ferrario et al., 1993, 1998; Budai et al., 2003; Božič et al., 2009; Baab et al., 2010), avšak růst obličejí není izometrický proces.

Pohlavní dimorfismus je evidentní jak ve velikosti, tak i ve tvaru obličejí (Hennessy et al., 2002; Evison et al., 2010). Vzájemný vztah tvaru a velikosti je alometrický, bývá studován na základě centroid size (Rosas and Bastir, 2002; Kimmerle et al., 2008; Schaefer and Bookstein, 2009; Gonzalez et al., 2011; Weisensee and Jantz, 2011; Nikita, 2012). Rosas and Bastir (2002) popisují, že velikost a pohlaví lebky mají signifikantní vliv na tvar, oproti tomu Kimmerle et al. (2008) nezaznamenali významný vliv velikosti na tvar lebky.

V předkládané publikaci **Velemínská et al. (2012)** bylo naším cílem analyzovat vztah mezi velikostní a tvarovou variabilitou pohlavních znaků obličejí, a to pomocí 3D modelů obličejů mladých mužů a žen středoevropské populace. Dalším cílem bylo odhalení rozdílů průměrného mužského a ženského obličejí, pomocí vizualizace tvarových a velikostních

rozdílů za využití FESA (Finite element scaling analysis). Důvodem bylo ověření předpokladu, že k pohlavnímu dimorfismu tvaru přispívá alometrie méně než nealometrická složka variability. Zároveň jsme se snažili objasnit vývoj některých vybraných dimorfních znaků.

Za tímto účelem bylo pomocí nekontaktního InSpeck 3D digitizéru nasnímáno celkem sto jedinců z Čech (50 mužů průměrného věku 21,1 let a 50 žen průměrného věku 21,6 let). Šlo o dospělé studenty Přírodovědecké fakulty a Fakulty humanitních studií Karlovy Univerzity. Takto získané 3D modely obličeje, skládající se z množství dílčích jednotek (trojúhelníkových elementů), byly dále analyzovány pomocí metod geometrické morfometrie. Stejného počtu elementů bylo dosaženo pomocí Dense correspondence model analysis s využitím GPA (Generalized Procrustes analysis) a TPS (thin-plate spline) analýz (Hutton et al., 2001, 2003). Takto transformovaná data byla poté využita jako iniciální data pro multivariační analýzy.

PCA (principal component analysis) byla použita ke sledování vztahu mezi průměrnými mužskými a ženskými obličejí a jejich variability se zaměřením na takové komponenty faciální variability, které nejlépe vyjadřují pohlavní dimorfismus. Pro popsání vztahu mezi centroid size (vyjadřující alometrii) a tvarovými pohlavními znaky (nealometrické složky pohlavního dimorfismu) jsme použili lineární regresi. Diskriminační funkční analýza s cross-validací byla využita k ověření přesnosti určení pohlaví diskriminační funkce. Analýzy byly provedeny zvlášť na datech se zachovanou i normalizovanou velikostí. Barevné mapy ilustrující průměrné pohlavní rozdíly byly výstupem FESA (Finite element scaling analysis), kdy jsou zvlášť zobrazeny velikostní a tvarové (deformační) změny dílčích elementů.

V publikaci Velemínská et al. (2012) jsme dospěli k následujícím závěrům:

- Podstatnou část pohlavního dimorfismu sledovaného souboru tvořila statická alometrie. Velikost obličeje byla spojena s faciální prolongací; čím větší obličej, tím protáhlejší, malé obličeje byly oválnější. Větší obličeje měly zároveň nízké, ploché čelo, kratší interorbitální vzdálenost, konvexní tvar nosu a širší ústa a bradu; korespondovaly s více maskulinními znaky. Malé obličeje měly vyšší klenuté čelo, vzdálenější oči, konkávní nos a štíhlá ústa a bradu, což odpovídá více feminním znakům obličeje
- Pohlavně dimorfní znaky byly výraznější po odstranění velikosti znaku. Šířková proporcionalita obličeje byla vyjádřena nealometrickou částí pohlavního dimorfismu. Maskulinní obličeje měly nízké, úzké, ubíhající čelo a širší, konvexnější nos v kombinaci s nižším a širším dolním obličejem. Feminní obličeje měly vyšší, klenuté a široké čelo, větší interorbitální vzdálenost, užší konkávnější nos spolu s úzkým, nižším, méně prominujícím dolním obličejem
- Pro klasifikaci ženského obličeje byl významnější tvar obličeje (nealometrická část pohlavního dimorfismu). Po normalizaci velikosti byly muži variabilnější než ženy a téměř polovina z nich měla obličej podobný ženskému. Pro muže naopak byla klasifikace významněji svázána s centroid size (alometrickou složkou)
- Sledováním celkového pohlavního dimorfismu tvaru i velikosti bylo zjištěno následující: čelo u mužů bylo šikmější; oči, lokalizované hluboko oproti periorbitální oblasti, byly blíže u sebe. Pozice očí představuje silnější intersexuální rozdíl než glabella, nadočnicové oblouky či hřbet nosu. Hlubší pozice očí a jejich užší štěrbinu může být následek větší a více vystupující frontální dutiny u mužů

- Mužský nos byl větší, konvexní, více vystupující anteriorně, nosní dírky byly nápadně větší a rozšířené. Střední část obličeje byla relativně užší s méně prominujícími lícními kostmi s menším množstvím měkké tkáně na lících
- Dolní obličej byl u mužů širší s masivní, dobře vytvořenou, muskulaturou v okolí ústního otvoru. Pro muže byla typická široká prominující brada

2.3 Variabilita lebky v časovém horizontu svrchní paleolit - raný středověk - recent

V následujících studiích jsme se soustředili na porovnání velikostních a tvarových rozdílů lebky mezi různými populacemi pocházejícími z našeho území. Vzhledem k populačním migracím v průběhu posledních třiceti tisíc let, nelze hovořit přímo o příbuznosti sledovaných populací či o mikroevolučních změnách, ponecháváme tedy termín diachronních změn lebky na území České republiky. Předpokládáme jistou míru biologické kontinuity, podobně jako ji předpokládají genetické studie.

Velikost a tvar lebky, zejména její baze, je pod silnou kontrolou genetických mechanismů (Manfredi et al., 1997; Sperber, 2001; Johannsdottir et al., 2005), zároveň je však rozvoj těchto komponent výrazně ovlivňován environmentálními vlivy (Beals et al., 1984; Roseman, 2004; Harvati and Weaver, 2006; Pfeiffer, 2007; Stynder et al., 2007; Betti et al., 2010). Genetické studie se soustřeďují na stopy prehistorické příměsi v genomu recentní populace (Semino et al., 2000; Dupanloup et al., 2004; Bauchet et al., 2007), morfologický výsledek těchto procesů na kraniofaciálních datech však není zcela objasněn (Martínez-Abadías et al., 2006).

V Evropě jsou nejstarším nálezem moderního *Homo sapiens* 35 tisíc let staré pozůstatky tří jedinců z jeskyně Peștera cu Oase v Rumunsku (Trinkaus et al., 2003). Před 28 tisíci let už je moderní člověk v Evropě široce rozšířen (Trinkaus, 2005; Jurmain et al., 2008). Kontinuita osídlení střední Evropy od svrchního paleolitu dodnes byla sledována i na základě morfologie lebky (Vlček, 1991, 1996). Avšak podle některých autorů jsou morfometrické vztahy mezi lebkami svrchního paleolitu a moderní populace nedostatečným indikátorem pro stanovení příbuzenských vztahů, neboť genetické a morfometrické vztahy nejsou podle nich ve shodě (Van Vark, 1994; Van Vark et al., 2003). Podle jiných studií si však kraniofaciální morfologie a genetické markery naopak odpovídají (Howells, 1995; Relethford, 2002, 2009;

Rosenberg et al., 2002; Jantz and Owsley, 2003). Je zřejmé, že analýza variability kraniofaciálních dimenzí může indikovat genetické vztahy mezi různými populacemi, pomáhá objasnit evoluci populací a jejich adaptací na lokální podmínky (Bruner et al., 2004; Brace et al., 2006; Betti et al., 2010).

Mezi mnoho vlivů podílejících se na fenotypové variabilitě lebky patří rozvoj encefalizace (Lieberman et al., 2000; Bruner et al., 2003; Lieberman, 2011), vzpřímená poloha těla a bipedie (Lieberman, 2011), vliv stravy (Carlson and Van Gerven, 1977; Lieberman, 2011), nutriční stres (Pfeiffer, 2007; Stynder et al., 2007), klima (Roseman and Weaver, 2004; Harvati and Weaver, 2006), pohlavní dimorfismus (Borovanský, 1936; Lieberman, 2011), hustota populace (Sardi et al., 2004, 2006) a další environmentální vlivy.

Hlavní tvarové rozdíly lebek jsou soustředěny na vztahy v rámci délky lebeční klenby, vývoje okcipitální oblasti a oploštění obličeje, pro lebku anatomicky moderního člověka je typické zkrácení obličeje a neurokraniální globularita (Lieberman et al., 2002; Martínez-Abadías et al., 2006; Lieberman, 2011). Z pohledu diachronních trendů hrají tyto autapomorfie nejdůležitější roli ve vzájemných rozdílech recentních a paleolitických lebek. Všechny skupiny moderního evropského *Homo sapiens* jsou si ve tvaru lebky blízce příbuzné a odlišují se od robustnějších pleistocenních lebek. Rozdíly od současného kraniofaciálního tvaru jsou považovány za příspěvek neolitické populace k variabilitě současných evropských lebek (Brace et al., 2006).

Pro paleolitické soubory je typický výrazný velikostní pohlavní dimorfismus, zároveň jsou však relativně homogenní z hlediska tvaru (Trinkaus and Svoboda, 2006). Svrchně paleolitické lebky jsou obvykle větší než současné lebky (Jantz and Owsley, 2003). Kromě typicky prodlouženého neurokrania mají fosilní lebky relativně prodloužené tělo mandibuly vzhledem k jejímu rameni, výraznou protruzi horní a dolní čelisti a celkově větší anteriorotaci a konvexitu obličeje (Lahr, 1996; Vlček and Šmahel, 2002; Frayer et al., 2006; Lieberman,

2011). Oproti tomu vertikální proměnné jsou pod silnější genetickou kontrolou, heritabilita pravděpodobně více ovlivňuje antero-vertikální dimenze než posteriorní (Manfredi et al., 1997).

Sledujeme-li délku lebky v Čechách a na Moravě, od svrchního paleolitu, přes neolit, eneolit, Únětickou kulturu a středověk do současnosti, typickým znakem je brachycefalizace, s nejnižší průměrnou délkou lebky u současné populace. Zatímco výška lebky neolitu, eneolitu a Únětické kultury je v průměru srovnatelná se současnými lebkami, svrchně paleolitické a raně středověké lebky jsou signifikantně nižší (Chochol, 1964; Černý and Velemínský, 1998; Černý, 1999; Velemínská et al., 2008 b). Porovnání se středověkými českými lebkami 9. století a lebek 16. - 19. století ukázalo kratší délku větve a delší tělo mandibuly u svrchně paleolitických lebek (Hanáková et al., 1984; Drozdová, 1997; Velemínská et al., 2008 b).

V publikaci **Velemínská et al. (2008 a)** bylo naším cílem monitorování diachronních změn a variability velikosti a tvaru lebek střeoevropské populace od svrchního paleolitu po současnost a vymezení do jaké míry jsou tyto odchylky způsobeny pohlavním dimorfismem. Ověřovali jsme, zde je možné, pomocí zvolených metod, vysledovat nejtypičtější evoluční změny *Homo sapiens*, jako je rozvoj neurokranální globularity a snižování faciální konvexity (Lieberman et al., 2002). Vycházeli jsme z detailní kraniometrické analýzy fotografií pěti dospělých lebek z Předmostí v laterální projekci (mužské, P1, P3, P9 a ženské P4, P10) a jejich srovnání se současnými standardy (laterální rentgenogramy 52 mužů a 36 žen) a s metrickými daty třech mužských lebek z Dolních Věstonic (DV13, DV14 a DV16).

Celkem bylo sledováno 30 lineárních a angulárních proměnných. Pomocí z-skóre byla analyzována variabilita dimenzí a jednotlivých lebek z Předmostí oproti průměru referenčního

souboru. Podobnost předmostenských lebek s recentním souborem byla odhadnuta pomocí multivariační metody, klastrové analýzy.

V této studii jsme dospěli k těmto závěrům:

- Lebky z Předmostí se výrazně podobaly lebkám z Dolních Věstonic, oba soubory se signifikantně lišily od recentního souboru
- Hlavními oblastmi projevujícími tvarové rozdíly lebky mezi paleolitickými a recentními soubory byly změny v délce mozkovny, v rozvoji okcipitální oblasti a oploštění obličeje
- Nejrobustnější ze sledovaných paleolitických lebek byla mužská lebka P3, lišící se od ostatních paleolitických lebek v některých dimenzích i o více než 1SD. Přesto při sledování velikostních charakteristik všech osmi sledovaných jedinců z Předmostí a Dolních Věstonic nebyly celkové rozdíly signifikantní
- Pro sledované paleolitické lebky (zejména mužské) bylo typické prodloužené a snížené neurokranium, nižší čelo, výraznější nadočnicové oblouky a delší, zalomenější okcipitální oblast
- Na splachnokraniu měly paleolitické lebky výrazně delší tělo mandibuly vzhledem k jejímu rameni, výraznou protruzi obou čelistí vzhledem k bazi lebni spolu s anteriorotací obličeje a větší obličejovou konvexitou při zachování normálních mezičelistních vztahů
- Pohlavní dimorfismus byl výrazný ve velikosti lebek, mužské lebky byly robustnější s výraznějšími oblastmi svalových úponů, ženy měly mírně menší úhel mandibuly (dokonce menší než recentní standardy)

- Změny ve tvaru lebky mezi sledovanými soubory, jako je rozvoj neurokraniální globularity a snižování faciální konvexity, odpovídaly mikroevolučním sekulárním změnám, které jsou však méně výrazné

K podobným závěrům jsme dospěli při sledování diachronní variability tvaru lebky mezi raně středověkým a recentním souborem. Výsledky byly prezentovány na zahraničních kongresech (Velemínská et al., 2009; Bigoni et al., 2010 b) a dovoluujeme si je zde představit, neboť logicky navazují na předchozí publikaci. V těchto pracech jsme sledovali, zda lze typické evoluční změny (rozvoj neurokraniální globularity a zmírnění faciální konvexity) v časovém horizontu svrchní paleolit-recent vysledovat i v periodě středověk-recent, tentokrát pomocí analýzy tvaru metodami geometrické morfometrie. Zajímá nás nejen celkový tvar lebky, ale také mikroevoluční změny morfologie některých obličejových částí lebky.

V prvním příspěvku (Velemínská et al., 2009) byly analyzovány 3D koordináty 55 landmarků v oblasti lebeční klenby, baze a obličeje a 39 semi-landmarků podél mediální křivky na klenbě. Sledováno bylo 173 lebek raně středověkých (Mikulčice) a 136 moderních lebek (Pachnerova sbírka). V druhé studii (Bigoni et al., 2010 b) bylo analyzováno 10 nepárových a 15 párových ektokraniálních landmarků lebky jako celku, očí, oblasti nosu a patra u 185 středověkých (Mikulčice) a 133 moderních lebek (Pachnerova sbírka). Další analýzy zahrnovaly multivariační (MANOVA) a geometricko-morfometrické metody (GPA, PCA, TPS).

Dospěli jsme k těmto závěrům:

- Tvar raně středověkých a recentních lebek byl signifikantně odlišný ve všech sledovaných regionech (lebka jako celek, lebeční klenba, baze, obličej, oblast očí, nosu, patra)
- Směrem k současným lebkám byly pozorovány následující změny: širší neurokranium s oválnější mediální křivkou a plošší parietální a okcipitální oblastí, bod opistion se posouvá anteriorně, bod bregma posteriorně a bod lambda inferiorně. V oblasti baze došlo k inferiornímu posunu oblasti bradavčitého výběžku, superiornímu posunu bodu basion a zvětšila se vzdálenost mezi infratemporálními landmarky
- Na obličejovém skeletu došlo směrem k současnosti k těmto změnám: zúžení obličeje, retruze maxilly, zmenšení konvexity obličeje, oválnější očníce, zkrácení vzdálenosti mezi očnícemi, okraj očníce více v sagitálním směru, hlubší patro v zadní části, ale mělčí v přední části, více prominující nosní kůstky, zúžení oblasti nosního otvoru
- U sledovaných souborů lze vysledovat rozvoj neurokranialní globularity a zmírnění konvexity obličeje. Tyto mikroevoluční změny jsou sice méně výrazné, nicméně obdobné, jako jsou diachronní kranialní změny v periodě svrchní paleolit – současnost

Kapitola 3

Závěr

V této části dizertační práce shrnujeme závěry, ke kterým jsme dospěli studiem několika aspektů biologické variability časově vzdálených populací pocházejících z území České republiky. Sledovanými soubory byly svrchně paleolitické lebky z Předmostí u Přerova, raně středověké lebky a postkraniální skelety ze sídliště Mikulčice, sbírka lebek a postkraniálních skeletů z 30. let 20. století (Pachnerova sbírka) a RTG snímky a 3D povrchové modely lebek a obličejů současné české populace. Závěr vychází z výsledků předkládaných publikací (Bigoni et al., 2005, 2010 a; Kujanová et al., 2008; Velemínská et al., 2008 a, 2012), příspěvků na konferencích (Velemínská et al., 2009; Bigoni et al., 2010 b) a publikace v recenzním řízení (Bigoni et al.).

Hodnocení kosterní bilaterální asymetrie minulých populací je významným ukazatelem jejich životního stylu, prostředí, mechanického a environmentálního stresu a socioekonomických rozdílů mezi zkoumanými populacemi a také v rámci těchto populací. Je významnou součástí hodnocení skeletální variability na daném území.

Asymetrické používání končetin či žvýkacího aparátu v důsledku preference jedné strany pro dané úlohy, bývá vyjádřeno direkcionalní asymetrií kosterního materiálu. Její příspěvek k variabilitě skeletu je snížen symetrickou funkcí dané části těla. Direkcionalní asymetrie

kostí končetin dosahuje vyšších hodnot u populací se zvýšenou mechanickou zátěží, i v souvislosti s vyšším nutričním a jiným environmentálním stresem. Direkcionální asymetrie lebky odráží rozdílnou stravu různých socioekonomických skupin.

Fluktuální asymetrie skeletu odráží environmentální stres působící na populační skupiny v souvislosti s jejich rozdílným sociálním a ekonomickým postavením, je indikátorem variability populace. Fluktuální asymetrie roste vlivem negativních vlivů prostředí, různé morfologické znaky reagují na tento stres nestejně. Indikuje také pravděpodobnou rozdílnou socioekonomickou situaci žen a mužů raného středověku.

Kraniofaciální pohlavní dimorfismus je dán vzájemným vztahem tvaru a velikosti. Na lebce (bez mandibuly) nejlépe determinuje pohlaví tvar horního obličeje a tvar mozkovny analyzovaný na základě křivky v její mediánní rovině. Analýza tvaru metodami geometrické morfometrie odhalila některé dílčí pohlavní rozdíly, které je obtížné detekovat metricky, a jsou příliš subjektivní při vizuálním hodnocení, jako je nestejná orientace očních či celkový tvar mediánní křivky. Nejvýrazněji se pohlavní dimorfismus lebky a obličeje projevuje v oblasti dolní části obličeje, zejména brady a jařmových oblouků. Pohlavní rozdíly na obličeji jsou zřejmé i v oblasti čela, očních a nadočnicových oblouků, nosu a nosního otvoru, rtů a v celkových délkošírkových parametrech. Pozice očí představuje silnější intersexuální rozdíl než glabella, nadočnicové oblouky či hřbet nosu. Tvarové pohlavní rozdíly jsou markantnější po odstranění velikosti znaku.

Analýza změn ve tvaru a velikosti svrchně paleolitických, raně středověkých a současných lebek ukázala, že interpopulační variabilita je charakterizována změnami v délce mozkovny, rozvoje okcipitální oblasti a oploštění obličeje. Směrem k současnosti dochází k rozvoji neurokranialní globularity a snižování faciální konvexity. Tento trend je výrazný v časovém horizontu svrchní paleolit – recent, a méně výrazný avšak obdobný v horizontu raný středověk - recent.

Výsledky předkládaných studií dokazují, že kosterní asymetrie a pohlavní dimorfismus lebky patří mezi důležité aspekty fenotypové variability člověka a že kraniofaciální variabilita je významným ukazatelem změn morfologie lidské kostry v čase a prostoru.

Budoucí výzkumy lze orientovat směrem k maximálnímu využití metod geometrické morfometrie, které nabízí možnosti objektivního sledování jak velikosti tak tvaru, a lze je tedy využít k přesnějším analýzám asymetrie a pohlavního dimorfismu, zejména k odlišení patologických a nepatologických změn. Chtěli bychom se také zaměřit na další analýzy tvaru křivek, jako je mediánní křivka neurokrania a okraj očnic. Dále lze sledovat celé povrchové modely lebek, pro detailnější studium rozdílů mezi populacemi, pohlavími či pravou a levou stranou lebky. Máme v úmyslu využít tyto metody k porovnání ontogenetických změn lebky, vzhledem k tomu, že již máme digitalizovány 3D data dětských lebek počátku 20. století od fetálního období po 12 let uložených v depozitářích Anatomického ústavu 1. lékařské fakulty UK. Zároveň bychom se rádi zaměřili na sledování diachronních změn v dalších populacích s ohledem na zachovalost kosterního materiálu (Únětická kultura, Eneolit).

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Přílohy

Příloha A



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The occurrence of directional and fluctuating limb asymmetry in a recently identified collection of human bones

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Abstract. This study is based on the metric processing of, in particular, the long bones of the upper and lower limbs of a rare, identified collection of bones originating in the first half of the 20th century (143 males and 157 females). It concentrates on the study of fluctuating asymmetry (FA), antisymmetry, directional (DA) and cross asymmetry in the length parameters of the upper and lower limbs. The presence of antisymmetry has not been recorded in this assemblage. For the lower limbs, FA was found to occur more frequently than DA. The size of the FA reached negligible values given the size of the indicators (method after Palmer & Strobeck, 1986). Limb DA occurred more often, and with greater absolute differences, among women than among men; in all of the assessed bones it was more common in the upper limbs than the lower, in the majority of cases in favour of the right side. The most pronounced DA appeared in the humerus, with all dimensions showing significant differences between sides. The lengths of the forearm bones were also highly asymmetrical, while DA was apparent least often in the scapula. The clavicle is shorter and more robust on the right side. In the lower limbs significant differences were only noted in the femur, while DA was not found in the crural bones. Femur DA occurred in most cases favouring the left side, and only in some epiphyseal dimensions the right side was greater. More pronounced DA in the lower limbs was manifest in the diaphyseal and epiphyseal dimensions than in length parameters. The presence of cross asymmetry was not universally confirmed, this occurring only among men (with longer right or left humerus), in the lengths of the fibula and tibia.

■ fluctuating asymmetry, directional asymmetry, cross asymmetry, antisymmetry, identified modern collection of bones, sexual dimorphism

INTRODUCTION

Asymmetry, a fundamental characteristic of all living organisms, is defined as a deviation from the overall symmetry of the organism and its different parts in relation to the median plane of the body (Škvařilová 1999). It thus appears in skeletal human remains, and has been studied for many reasons; this study concentrates on asymmetry in the size and shape of long bones in the post-cranial human skeleton, and on the differentiation of their individual types. Asymmetry is one of the major markers of stress, developmental stability and unequal functional loads on the two sides of the body. Several studies have demonstrated that a certain degree of asymmetry is in fact the norm in the length of the humerus and fe-

mur (e.g. Helmkamp & Falk 1990), while the genetic basis of asymmetry, its ontogenesis and the influences of age, sex and external environment have also been studied.

At the present time three basic types of asymmetry are distinguished for the variability of bilateral markers: directional asymmetry, fluctuating asymmetry and antisymmetry, arising out of different causes (Van Valen 1962, Palmer & Strobeck 1986, Palmer 1994; see Fig. 1).

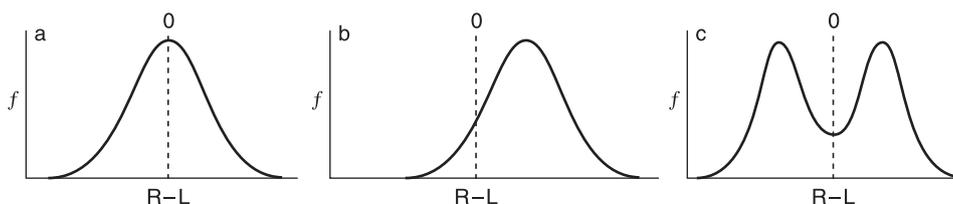


Fig. 1. Distribution of right-left difference in bilateral organisms: (a) FA, (b) DA, (c) antisymmetry (Palmer 1994).

Directional asymmetry (DA) displays itself in the preponderance of a given marker on the right or left side in the sample. This is a bilateral asymmetry, where the average deviation of the marker from the right and left sides in the studied collection is always greater or less than zero. A distribution of differences of the right and left sides is normal. The most conspicuous example in the human skeleton is to be found in the longer and more robust right upper and left lower limb, in connection with the functional laterality of the limbs (Schell et al. 1985, Škvařilová 1999, Čuk et al. 2001). Some authors hold that it is possible that DA is found very early in ontogenesis (Schultz 1937, Pande & Singh 1971) and that it develops further (in childhood – Van Dusen 1939; in adolescence – Schell et al. 1985, and in adulthood – Laubach & McConville 1967, Malina & Buschang 1984), for example in association with biomechanical factors acting differently on the two sides of the body. The most significant cause of asymmetrical development of the upper limbs in particular is regarded as being handedness (i.e. the preference for one – the right or left – upper limb; right- and left-handedness respectively). This is the influence of a high mechanical load placed during life asymmetrically on one side of the body (Ruff & Jones 1981, Schell et al. 1985, Roy et al. 1994, Steele & Mays 1995, Škvařilová 1999, Čuk et al. 2001). The causes of the occurrence of DA may also, however, have a genetic basis (Schultz 1937, Stirland 1993). Environmental stress is an important factor (Albert & Greene 1999), while ontogenetic factors linked to age and sex (Helmkamp & Falk 1990, Stirland 1993) evidently have an influence, too. Among children a dependency of DA upon age has been identified, but not upon sex (Škvařilová 1999). Many works have found no difference in the development of asymmetry between the sexes (Steele & Mays 1995, Plochocki 2002), while others indicate greater asymmetry rather among women (Schultz 1937), but sometimes among men (adolescents – Schell et al. 1985).

Fluctuating asymmetry (FA) is the type of bilateral asymmetry, which occurs when the deviations of the right and left sides in a sample are normally distributed around a mean of zero (Palmer 1994). It is probably caused by instability during ontogenesis (developmental noise), which developmental stability (the ability of the organism to create ideal/symmetrical forms under a particular set of environmental conditions; Zakharov & Graham 1992) and canalization (the ability of the organism to develop along an ideal de-

developmental trajectory under diverse environmental conditions; Palmer 1994 attempt to counteract or buffer. FA has thus been taken as a measure of the developmental stability, health and fitness of the organisms and the environmental stresses acting upon them (Palmer & Strobeck 1986, Zakharov & Graham 1992, Albert & Greene 1999). Environmental stress (temperature extremes, a polluted environment, parasitism, nourishment, population density etc.) increases FA (Zakharov & Graham 1992, Palmer 1994). FA has no genetic basis, but several genetic factors may of course increase it (inbreeding, lower heterozygosity, mutation etc.; Livshits & Kobylansky 1989, 1991).

Antisymmetry has a platykurtic or bimodal distribution of left-right difference around a mean of zero; in other words, one side always predominates (in terms of significant differences), but which it is – whether right or left – is variable (Van Valen 1962).

A further aim of this project was to establish the presence of cross asymmetry; this is a relationship between the asymmetry of the upper and lower limbs, where for example an individual with a longer and more robust right humerus also has longer and more robust bones in the lower left limb, or vice versa. Moreover, according to some authors right-handed individuals have a more developed right upper limb and left-handers a more developed left upper limb (Ingelmark 1946, Siniarska & Sarna 1980, Ruff & Jones 1981, Steele & Mays 1995). According to some studies the size dominance of the upper right limb is associated with handedness (Steele & Mays 1995), while the lower left limb is larger regardless of the hand preference (Macho 1991). The authors therefore divide the lower limbs into supportive leg and dominant leg, which demonstrated cross asymmetry of tibia with humerus. The supportive leg is in most cases the left, the left femur having a stronger diaphysis; in contrast, the right femur has a greater epicondylar width, showing that greater loads are placed on the non-supportive leg at the knee (Singh 1970, Plato et al. 1985, Macho 1991, Čuk et al. 2001).

Research into bone asymmetry first appeared in the professional literature as early as during the 19th century. The first study of bone asymmetry was probably that by the anatomist Philipp Friedrich Arnold in 1844 (Škvařilová 1999), which revealed the dominance of the right humerus and forearm bones and the left femur in length. In general, a greater absolute symmetry in the lengths of different segments of the upper and lower extremity was reported than asymmetry in the total length of the extremity (Jurowska 1972). Thus far all studies have demonstrated the fact that the most conspicuous bilateral bone asymmetry appears in the bones of the upper limb, while that of the lower limb is less obvious. The reason for this is probably the very asymmetric loads on the upper limbs associated with handedness, while the lower limbs are used more or less evenly e.g. in walking (Schell et al. 1985, Čuk et al. 2001). Some authors believe that the degree of asymmetry reflects the size of the load placed on the given limb, while localisation of the asymmetry indicates the type of effort exerted (Čuk et al. 2001).

DA is more frequent than FA in the upper limbs (Škvařilová 1999). In the upper limb DA is expressed, according to most studies, in the longer and more robust bones of the right side, and mainly in connection with asymmetric loads on the upper limbs (e.g. Stirland 1993, 1998, Steele & Mays 1995, Čuk et al. 2001). Only the clavicle is, particularly among adult individuals, shorter and more robust on the right side, probably thanks to massive development of the muscles at this location at the expense of its growth (Mays et al. 1999). The most asymmetric bone is the humerus (e.g. Čuk et al. 2001). Some studies indicate that the proximal epiphysis of the humerus is more asymmetric than the distal, while in the bones of the forearm the situation is reversed. It seems clear to the author

that the wrist and shoulder are more asymmetrically stressed than the elbow (Čuk et al. 2001). It would seem that among right-handed individuals DA favours the right upper limb, while among left-handers it favours the left limb (Ingelmark 1946, Steele & Mays 1995, Čuk et al. 2001). In modern European society around 80–82 % of the population are right-handed, while 15 % are left-handed and 3–5 % exhibit no preference (Annett & Kilshaw 1983). The same figures come out of several studies of skeletal material where handedness is unknown (Schultz 1937, Steele & Mays 1995, Čuk et al. 2001), where the individuals concerned are divided according to the length of the humerus into probable right- and left-handed. Although it is only in the present that there have been relaxed cultural pressures against left-handedness and the percentage of left-handers in society is gradually increasing (Fleminger et al. 1977, Steele & Mays 1995), in the skeletal material the representation is relatively stable. It is likely that asymmetry in bone development is a reflection of the loads arising out of repetitive or power tasks, rather than fine manipulation such as writing; for this reason skeletal DA may be more resistant to cultural pressures for handedness switching (Steele & Mays 1995).

Studies of asymmetry in the lower limbs generally show a heavier and more robust left lower limb, regardless of the handedness (Latimer & Lowrance 1965, Singh 1970, Macho 1991). In studying the asymmetry of the femur, the authors in most instances come to the conclusion that the left femur has the usual stronger diaphysis (particularly among women) and is heavier than the right, but that DA is not apparent in the length of the bone (Ruff & Hayes 1983, Macho 1991, Ruff 1992). This may be connected with the fact that the length growth of the bone concludes between the 18th and 25th year, while width growth undergo biomechanical influences throughout life (Čuk et al. 2001). Furthermore, several studies speak of “more rounded” diaphyses of the right femur (Macho 1991). According to these results the femur should be regarded as an expression of the left lower limb as the supportive and load-bearing leg, again regardless of the handedness (Macho 1991, Čuk et al. 2001). The right lower limb is used for more specific tasks (e.g. kicking), and the load is applied in particular to the knee; DA thus appears in several epiphyseal dimensions to favour the right side (Čuk et al. 2001). In contrast, in the study by Čuk et al. (2001) the tibia exhibits cross asymmetry with humerus, i.e. a longer right humerus/longer left tibia and vice versa. The leg with a more supportive function (characterised by a more developed femur) is thus in most cases the left, while the dominant leg (expressed by a more developed tibia) is, depending on handedness, for right-handers generally the left and vice versa.

MATERIALS AND METHODS

Bones were studied in the modern osteological assemblage so-called Pachner collection dated to the 1930s. It originated under the direction of Professor Pachner for the purposes of studying sexual indicators in the human pelvis at the Institute of Anatomy of the First Medical Faculty of Charles University in Prague, Czechoslovakia. Originally the postcranial skeletons of 100 females and 115 males were studied post mortem; later the collection was expanded to 305, now regrettably incomplete, skeletons of adult individuals. The advantage of working with this collection is the excellent degree of preservation of the majority of the bones, and the identifications of the skeletons (sex, height, age, name, year of autopsy, in some cases cause of death etc.). The only skeletons not included in the analysis were those with pathological deformations and those for which sex was not recorded. This meant that for this study of asymmetry the skeletal remains of a total

of 157 women and 143 men were measured. The assemblage cannot be considered to be a sample for a normal, modern population, as these are all adult individuals of the lower social orders (Pachner 1937). At the present time the greater part of the collection is stored in the osteological depository of the Department of Anthropology and Human Genetics of the Faculty of Natural Sciences at Charles University in Prague, Czech Republic, with the rest in the collections of the Institute of Anatomy of the First Medical Faculty at Charles University in Prague.

The metric characteristics of the bones were selected such that they most precisely described their sizes and shapes with regard to robusticity and degree of preservation. The precisely defined dimensions were taken following Martin & Saller (1957–1962) and Velemínský (2000). All of the surviving limb bones in the collection were metrically processed. From the upper limb, the clavicle, scapula, humerus, radius and ulna were studied; from the lower limb the femur, tibia and fibula. A total of 27 linear and circumferential metric characteristics were measured for the lower limb and 21 for the upper (for the dimensions see Tabs 1, 3). The assemblage of adult skeletal remains was not divided into exact age categories. Given the size of the assemblage and the conspicuous sexual dimorphism, all data were processed separately for men and women.

Basic statistical indicators were calculated for all of the data obtained. The reliability of the measurements was verified by the repeated measurement of 16 individuals (Steele & Mays 1995, Mays et al. 1999), with consideration given to inter-individual error (reliability coefficient) and to systematic error (paired t-test). Testing using ANOVA revealed that the FA was not conditioned by measurement error (Little et al. 2002, Roy et al. 1994). A t-test for independent samples was employed to compare size differences between men and women. The normal distribution of right-left differences and the consequent ruling out of the presence of antisymmetry (bimodal or platykurtic curve) were verified graphically. Given the size of the data set it is not possible to publish all of these calculations here, but along with others they are included in the theses by Fialová (2004) and Žaloudková (2004).

A paired t-test was used for the actual establishing of directional asymmetry. The null hypothesis of the coincidence of the population right and left side average was tested to a 5 % significance level, and significant differences were regarded as being directional asymmetry. Other deviations from symmetry were adjudged to be fluctuating asymmetry, after the approach of Škvařilová (1999).

Only for those dimensions where the presence of DA and antisymmetry had been ruled out was the size of the FA established with the aid of models from Palmer & Strobeck (1986); the presence of DA or antisymmetry could have impaired the calculation of FA (Palmer & Strobeck 1986). The FA1 and FA2 models, which yield information on absolute asymmetry, were employed, as were FA4 and FA6, which are suitable for establishing the signed asymmetry. At the same time, FA2 and FA6 are not biased by size-dependence of the right-left difference.

FA1: $\text{mean } |R-L|$

FA2: $\text{mean } \{|R-L| / [(R+L) / 2]\}$

FA4: $\text{var } (R-L)$

FA6: $\text{var } \{(R-L) / [(R+L) / 2]\}$

The presence of cross asymmetry (where a given individual would have both longer right upper and left lower limb, or vice versa) was tested on the basis of the maximum lengths of the humerus, femur, tibia and fibula. The individuals were divided on the basis of humerus length into those with a longer right/left humerus (hypothetically right-

and left-handers respectively; Steele & Mays 1995, Čuk et al. 2001). Within these “groups” the proportion of individuals with longer right/left lower limb bones was then assessed.

The data obtained were processed using Statistica Base 6 and Microsoft Excel 2003 software.

RESULTS

Measurement reliability was tested through the use of the reliability coefficient, ANOVA and systematic error testing, and showed the high degree of reliability of the repeated measurements. Reliability coefficient has never decreased below the value 0.8, thus all measurements were meaningful. The ANOVA revealed no differences between the first and second measurements of the right and left sides; the variability between the indicators is therefore not caused by measurement error. Asymmetry was established separately for both sexes, as in all of the indicators studied men were highly significantly larger than women (Fialová 2004, Žaloudková 2004).

Study of asymmetry

The graphic depiction (Fig. 2) of the right-left differences in individual dimensions confirms the normal distribution of said differences. The presence of asymmetry was thus ruled out in all cases, as no distribution was platykurtic or bimodal.

DA appears far more often in the upper limb than in the lower. In the upper limb DA generally trends towards the right (with the exception of clavicle length), and in the lower to the left (with the exception of some epiphyseal dimensions).

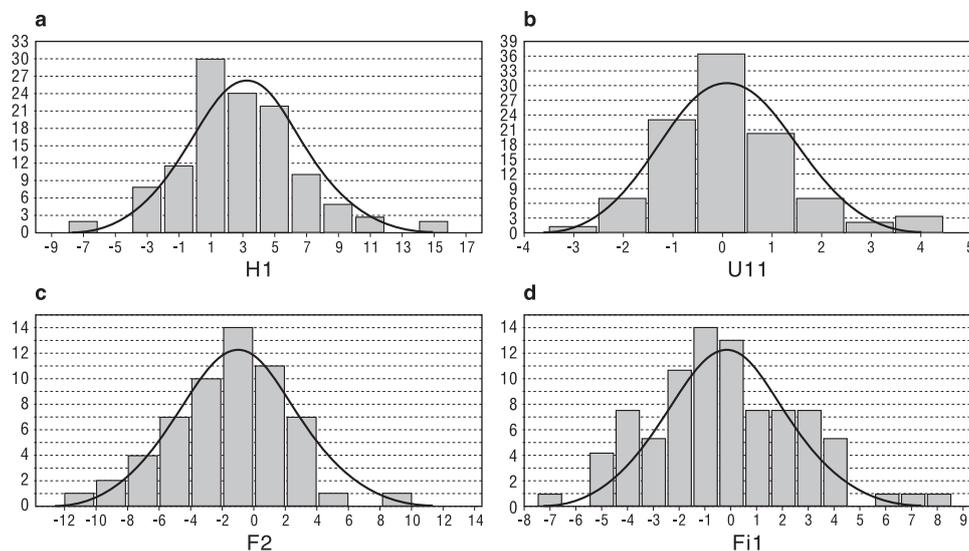


Fig. 2. Examples of the graphic depiction of the distribution of right-left differences.
 a – H1 (maximum length of the humerus) – DA trends towards the right; males (N = 117)
 b – U11 (sagittal diameter of the diaphysis of the ulna) – FA; males (N = 103)
 c – F2 (physiological length of the femur) – DA trends towards the left; females (N = 58)
 d – Fi1 (maximum length of the fibula) – FA; females (N = 81)

Table 1. DA: Results of paired t-tests of the dimensions of the upper limbs of males (diameters given in mm; SD – standard deviation, N – number of dimensions, t – value of the t-test (df = N-1), p – test level attained; significance levels: * = 0.05, ** = 0.01, * = 0.001).**

			Mean	SD	N	t	p		
SCAPULA	anatomical width	Sc1	sin	161.9	9.10				
		dx	161.3	8.55	80	1.334	0.186		
	anatomical length	Sc2	sin	104.6	6.29				
		dx	104.0	5.83	112	3.104	0.002	**	sin
	length of the margo lateralis	Sc3	sin	138.3	8.06				
		dx	138.0	8.53	112	1.000	0.319		
CLAVICULA	maximum clavicle length	C11	sin	150.8	7.97				
		dx	149.2	7.82	97	3.334	0.001	**	sin
	vertical diameter	C14	sin	11.1	1.29				
		dx	11.3	1.47	112	-1.815	0.072		
	sagittal diameter	C15	sin	12.6	1.44				
		dx	13.0	1.36	112	-3.040	0.003	**	dx
HUMERUS	maximum length of the humerus	H1	sin	322.4	17.30				
		dx	325.7	16.71	117	-9.933	0.000	***	dx
	width of the upper epiphysis	H3	sin	50.5	2.33				
		dx	51.4	2.34	118	-8.274	0.000	***	dx
	width of the lower epiphysis	H4	sin	61.7	3.77				
		dx	62.2	3.86	118	-3.544	0.001	***	dx
	maximum diameter of the middle of the diaphysis	H5	sin	23.2	1.93				
		dx	23.8	2.05	120	-5.344	0.000	***	dx
	minimum diameter of the middle of the diaphysis	H6	sin	18.6	1.67				
		dx	18.9	1.69	120	-4.698	0.000	***	dx
maximum transverse diameter of the head	H9	sin	44.3	2.05					
	dx	44.7	2.26	112	-3.145	0.002	**	dx	
maximum vertical diameter of the head	H10	sin	48.0	2.37					
	dx	48.5	2.22	118	-4.148	0.000	***	dx	
ULNA	maximum length of the ulna	U1	sin	255.4	13.18				
		dx	257.5	13.08	100	-6.387	0.000	***	dx
	sagittal diameter of the diaphysis	U11	sin	14.3	1.27				
		dx	14.4	1.39	103	-0.904	0.368		
	width of the diaphysis	U12	sin	17.5	1.39				
		dx	17.7	1.49	103	-1.618	0.109		
RADIUS	maximum length of the radius	R1	sin	237.0	11.92				
		dx	239.7	12.04	96	-8.445	0.000	***	dx
	maximum width of the diaphysis	R4	sin	17.8	1.57				
		dx	18.2	1.74	97	-3.523	0.001	***	dx
	sagittal diameter of the diaphysis	R5	sin	12.4	1.12				
		dx	12.5	1.11	97	-1.026	0.308		
	width of the middle of the diaphysis	R4a	sin	16.7	1.57				
		dx	17.3	1.63	98	-4.570	0.000	***	dx
sagittal diameter of the middle of the diaphysis	R5a	sin	12.7	1.07					
	dx	12.8	1.00	98	-1.440	0.153			

In the upper limb (Tabs. 1, 2) DA is present in all of the studied bones, among a total of 74 % of the metric indicators studied. DA appeared most conspicuously, and in all dimensions, on the humerus, and is also obvious in the maximum lengths of the forearm bones; it was found least often in the scapula. Men mostly have a greater length of the left scapula, and in women a longer length of the margo lateralis of the right scapula is present. The majority of the individuals have a shorter and more robust right clavicle, the sagittal diameter of the clavicle is on average greater on the right side. The humerus is

Table 2. DA: Results of paired t-tests of the dimensions of the upper limbs of females (for legend see Tab. 1).

				Mean	SD	N	t	p			
SCAPULA	anatomical width	Sc1	sin	144.3	9.00						
			dx	144.4	8.92	78	-0.076	0.939			
	anatomical length	Sc2	sin	96.6	5.50						
			dx	96.7	5.56	112	-0.343	0.733			
	length of the margo lateralis	Sc3	sin	125.2	8.86						
			dx	126.3	8.81	106	-4.003	0.000	***	dx	
CLAVICULA	maximum clavicle length	Cl1	sin	136.1	7.11						
			dx	134.4	7.14	75	4.548	0.000	***	sin	
	vertical diameter	Cl4	sin	9.1	1.29						
			dx	9.2	1.22	108	-0.465	0.643			
	sagittal diameter	Cl5	sin	10.9	1.16						
			dx	11.4	1.28	108	-4.696	0.000	***	dx	
HUMERUS	maximum length of the humerus	H1	sin	297.7	15.19						
			dx	301.2	15.24	125	-10.003	0.000	***	dx	
	width of the upper epiphysis	H3	sin	44.8	2.47						
			dx	45.5	2.59	125	-7.016	0.000	***	dx	
	width of the lower epiphysis	H4	sin	54.0	3.19						
			dx	54.8	3.33	126	-5.608	0.000	***	dx	
	maximum diameter of the middle of the diaph.	H5	sin	20.6	1.65						
			dx	21.2	1.64	127	-6.655	0.000	***	dx	
	minimum diameter of the middle of the diaph.	H6	sin	16.2	1.36						
			dx	16.4	1.50	127	-3.675	0.000	***	dx	
	maximum transverse diameter of the head	H9	sin	39.0	1.97						
			dx	39.5	2.19	112	-4.578	0.000	***	dx	
maximum vertical diameter of the head	H10	sin	42.1	2.24							
		dx	42.5	2.54	119	-3.214	0.002	**	dx		
ULNA	maximum length of the ulna	U1	sin	230.8	11.56						
			dx	234.0	12.18	118	-10.806	0.000	***	dx	
	sagittal diameter of the diaphysis	U11	sin	11.9	1.09						
			dx	12.2	1.07	126	-4.024	0.000	***	dx	
	width of the diaphysis	U12	sin	15.0	1.24						
			dx	15.3	1.25	126	-4.887	0.000	***	dx	
RADIUS	maximum length of the radius	R1	sin	212.8	11.67						
			dx	216.3	12.17	123	-9.617	0.000	***	dx	
	maximum width of the diaphysis	R4	sin	15.6	1.61						
			dx	15.9	1.53	128	-4.078	0.000	***	dx	
	sagittal diameter of the diaphysis	R5	sin	10.6	0.81						
			dx	10.6	0.80	128	-0.961	0.338			
	width of the middle of the diaphysis	R4a	sin	14.7	1.44						
			dx	15.1	1.43	128	-6.121	0.000	***	dx	
sagittal diameter of the middle of the diaphysis	R5a	sin	10.6	0.77							
		dx	10.7	0.79	128	-2.350	0.020	*	dx		

markedly asymmetrical in all dimensions in both men and women, in every case in favour of the right side. The greatest differences occur in the average values of maximum length in the humerus; men have a right humerus longer by an average of 3.3 mm, and women 3.5 mm. In the male forearm bones DA appears primarily in the lengths as well as in the width of the diaphysis of the radius. Among women DA appears in almost all dimensions of the forearm bones (the average differences in bone length being 3.5 mm). In all cases the right side is dominant in the bones of the forearm. While the differences between the sexes are not overly pronounced, greater differences were nevertheless observed in the average dimension values among women.

Table 3. DA: Results of paired t-test of the dimensions of the lower limbs of males (for legend see Tab. 1).

				Mean	SD	N	t	p		
FEMUR	maximum length of the femur	F1	sin	451.8	23.47					
			dx	450.9	22.83	66	1.457	0.150		
	physiological length	F2	sin	449.7	23.20					
			dx	448.0	22.62	66	2.761	0.007	**	sin
	sagittal diameter of the middle of the diaphysis	F6a	sin	28.5	2.43					
			dx	28.7	2.49	67	-1.130	0.262		
	transverse diameter of the middle of the diaphysis	F7a	sin	28.6	2.42					
			dx	28.5	2.33	67	0.639	0.525		
	upper transverse diameter of the diaphysis	F7b	sin	30.8	2.67					
			dx	30.6	2.69	67	1.390	0.169		
	upper sagittal diameter of the diaphysis	F7c	sin	28.7	2.21					
			dx	28.0	2.26	67	5.457	0.000	***	sin
	lower transverse diameter of the diaphysis	F7d	sin	35.9	3.96					
			dx	35.7	4.10	67	0.878	0.383		
	lower sagittal diameter of the diaphysis	F7e	sin	31.7	3.06					
			dx	31.1	2.94	67	4.243	0.000	***	sin
	subtrochanteric transverse diameter of the diaph.	F9	sin	33.7	2.62					
			dx	33.7	2.60	67	-0.168	0.867		
	subtrochanteric sagittal diameter of the diaphysis	F10	sin	28.9	2.19					
dx			28.5	2.24	67	2.690	0.009	**	sin	
circumference of the middle of the diaphysis	F8	sin	87.3	5.68						
		dx	87.2	5.67	67	0.521	0.604			
upper width of the epiphysis	F13	sin	101.8	6.25						
		dx	102.0	5.92	66	-0.327	0.745			
epicondylar width	F21	sin	82.1	4.52						
		dx	82.8	4.54	67	-3.339	0.001	**	dx	
vertical diameter of the head	F18	sin	48.6	2.59						
		dx	48.8	2.68	66	-0.976	0.333			
transverse diameter of the head	F19	sin	48.3	2.45						
		dx	48.4	2.67	66	-0.757	0.452			
FIBULA	maximum length of the fibula	Fil	sin	359.2	24.55					
			dx	359.3	23.77	93	-0.170	0.865		
TIBIA	overall length tibiae	T1	sin	367.2	21.43					
			dx	367.7	20.76	47	-0.622	0.537		
	medial length	T1b	sin	356.8	20.32					
			dx	357.5	20.48	46	-0.811	0.422		
	maximum width of the upper epiphysis	T3	sin	74.6	2.92					
			dx	74.2	2.99	46	2.008	0.051		
	width of the lower epiphysis	T6	sin	48.5	3.02					
			dx	48.1	2.88	47	1.449	0.154		
	minimum diameter of the middle of the diaphysis	T8	sin	29.4	2.73					
			dx	29.5	2.32	53	-0.855	0.396		
	width of the middle of the diaphysis	T9	sin	22.7	1.95					
			dx	22.6	2.09	53	0.484	0.630		
	sagittal diameter in the upper foramen nutricium	T8a	sin	33.8	3.28					
			dx	33.7	2.98	51	0.409	0.684		
	width of the diaphysis in the upper for. nutric.	T9a	sin	25.0	2.12					
			dx	25.1	2.40	51	-0.461	0.647		
circumference of the middle of the diaphysis	T10	sin	80.4	5.87						
		dx	79.8	5.61	53	1.965	0.055			
circumference of the diaphysis on the for. nutric.	T10a	sin	91.2	7.34						
		dx	91.0	6.81	51	0.446	0.657			
minimum circumference of the diaphysis	T10b	sin	71.8	5.10						
		dx	71.7	4.91	53	0.778	0.440			

Table 4. DA: Results of paired t-tests of the dimensions of the lower limbs of females (for legend see Tab. 1).

			Mean	SD	N	t	p		
FEMUR	maximum length of the femur	F1	sin	415.0	19.17				
			dx	414.6	19.59	58	0.681	0.499	
	physiological length	F2	sin	411.6	19.33				
			dx	410.5	19.81	58	2.106	0.040	*
	sagittal diameter of the middle of the diaphysis	F6a	sin	25.9	2.00				
			dx	25.9	2.19	64	-0.244	0.808	
	transverse diameter of the middle of the diaphysis	F7a	sin	26.8	2.50				
			dx	26.5	2.23	64	2.116	0.038	*
	upper transverse diameter of the diaphysis	F7b	sin	29.3	2.55				
			dx	28.6	2.76	64	3.550	0.001	***
	upper sagittal diameter of the diaphysis	F7c	sin	25.7	2.29				
			dx	25.2	2.06	64	2.657	0.010	**
	lower transverse diameter of the diaphysis	F7d	sin	33.0	3.71				
			dx	33.0	3.76	64	0.000	1.000	
	lower sagittal diameter of the diaphysis	F7e	sin	28.7	2.23				
			dx	28.0	2.42	64	3.832	0.000	***
	subtrochanteric transverse diameter of the diaph.	F9	sin	31.5	2.30				
			dx	31.2	2.52	63	1.474	0.146	
	subtrochanteric sagittal diameter of the diaphysis	F10	sin	25.9	1.90				
			dx	25.9	2.16	63	0.000	1.000	
circumference of the middle of the diaphysis	F8	sin	80.2	5.91					
		dx	79.6	5.60	65	2.100	0.040	*	sin
upper width of the epiphysis	F13	sin	88.1	5.62					
		dx	88.6	5.85	59	-2.151	0.036	*	dx
epicondylar width	F21	sin	73.8	3.93					
		dx	73.9	3.75	59	-0.769	0.445		
vertical diameter of the head	F18	sin	43.1	2.80					
		dx	43.1	2.87	58	-0.136	0.892		
transverse diameter of the head	F19	sin	42.5	2.18					
		dx	42.7	2.27	58	-1.763	0.083		
FIBULA	maximum length of the fibula	Fi1	sin	328.6	16.43				
			dx	328.3	16.60	81	0.762	0.449	
TIBIA	overall length tibiae	T1	sin	338.5	17.50				
			dx	337.9	17.24	63	1.257	0.214	
	medial length	T1b	sin	329.4	17.65				
			dx	328.9	17.42	59	1.137	0.260	
	maximum width of the upper epiphysis	T3	sin	66.7	3.40				
			dx	66.6	3.70	55	0.457	0.649	
	width of the lower epiphysis	T6	sin	44.0	2.64				
			dx	44.1	2.71	54	-0.339	0.736	
	minimum diameter of the middle of the diaphysis	T8	sin	26.6	2.40				
			dx	26.7	2.54	69	-0.173	0.863	
	width of the middle of the diaphysis	T9	sin	20.6	1.88				
			dx	20.8	2.33	69	-1.396	0.167	
	sagittal diameter in the upper foramen nutricium	T8a	sin	29.9	2.56				
			dx	29.9	2.52	69	0.346	0.730	
	width of the diaphysis in the upper for. nutric.	T9a	sin	22.2	1.98				
			dx	22.3	2.30	69	-0.956	0.343	
	circumference of the middle of the diaphysis	T10	sin	72.1	4.91				
			dx	72.1	6.01	70	-0.082	0.935	
	circumference of the diaphysis on the for. nutric.	T10a	sin	80.8	5.42				
			dx	80.9	6.06	70	-0.271	0.788	
minimum circumference of the diaphysis	T10b	sin	65.5	4.45					
		dx	65.6	4.85	71	-0.518	0.606		

Table 5. Results of evaluation of the FA of the dimensions of the upper limbs (FA1, FA2, FA4, FA6: indices of the calculation of FA values, see section on 'Materials and methods'; DA – dimension for which DA presence was found).

			male				female			
			FA1	FA2	FA4	FA6	FA1	FA2	FA4	FA6
SCAPULA	anatomical width	Sc1	2.925	0.018	13.423	0.001	2.981	0.015	19.230	0.001
	anatomical length	Sc2	DA	DA	DA	DA	1.723	0.018	6.110	0.001
	length of the margo lateralis	Sc3	2.304	0.017	8.917	0.000	DA	DA	DA	DA
CLAVICULA	maximum clavicle length	C11	DA	DA	DA	DA	DA	DA	DA	DA
	vertical diameter	C14	0.821	0.073	1.301	0.010	0.713	0.078	1.063	0.013
	sagittal diameter	C15	DA	DA	DA	DA	DA	DA	DA	DA
HUMERUS	maximum length of the humerus	H1	DA	DA	DA	DA	DA	DA	DA	DA
	width of the upper epiphysis	H3	DA	DA	DA	DA	DA	DA	DA	DA
	width of the lower epiphysis	H4	DA	DA	DA	DA	DA	DA	DA	DA
	maximum diameter of the middle of the diaphysis	H5	DA	DA	DA	DA	DA	DA	DA	DA
	minimum diameter of the middle of the diaphysis	H6	DA	DA	DA	DA	DA	DA	DA	DA
	maximum transverse diameter of the head	H9	DA	DA	DA	DA	DA	DA	DA	DA
	maximum vertical diameter of the head	H10	DA	DA	DA	DA	DA	DA	DA	DA
ULNA	maximum length of the ulna	U1	DA	DA	DA	DA	DA	DA	DA	DA
	sagittal diameter of the diaphysis	U11	0.913	0.063	1.695	0.008	DA	DA	DA	DA
	width of the diaphysis	U12	0.602	0.034	0.719	0.002	DA	DA	DA	DA
RADIUS	maximum length of the radius	R1	DA	DA	DA	DA	DA	DA	DA	DA
	maximum width of the diaphysis	R4	DA	DA	DA	DA	DA	DA	DA	DA
	sagittal diameter of the diaphysis	R5	0.608	0.049	0.785	0.005	0.383	0.035	0.411	0.004
	width of the middle of the diaphysis	R4a	DA	DA	DA	DA	DA	DA	DA	DA
	sagittal diameter of the middle of the diaphysis	R5a	0.541	0.042	0.589	0.004	DA	DA	DA	DA

In the lower limb (Tabs. 3, 4) DA was recorded only in the size characteristics of the femur, specifically in 47 % of the studied dimensions among women and 33 % among men. The women in this assemblage from a modern population are thus more asymmetrical than the men. DA could not be demonstrated in the fibula or tibia. In both sexes femur DA was observed in the dimensions of length and of the diaphysis in favour of the left side, and in the dimensions of the epiphysis in favour of the right side. Significant differences in sides (trending to the left) were recorded in men only in the physiological length and in all sagittal diameters of the femur shape; among women they were also found in the transversal diameters of the shape and circumference of the diaphysis. DA towards the right was recorded in men in the epicondylar width, and in women in the upper width of the epiphysis.

The size of FA (Tabs. 5, 6) was evaluated only for those dimensions where the presence of DA had already been ruled out. FA occurred more often in the lower limb than in the upper. The variance or absolute deviation of the FA, which is sensitive to size-dependence of the right-left difference (FA1, FA4), reached its greatest values in the dimensions

Table 6. Results of evaluation of the FA of the dimensions of the lower limbs (FA1, FA2, FA4, FA6: indices of the calculation of FA values, see section on 'Materials and methods'; DA – dimension for which DA presence was found).

			male				female			
			FA1	FA2	FA4	FA6	FA1	FA2	FA4	FA6
FEMUR	maximum length of the femur	F1	3.500	0.008	22.845	0.000	3.517	0.008	21.070	0.000
	physiological length	F2	DA	DA	DA	DA	DA	DA	DA	DA
	sagittal diameter of the middle of the diaphysis	F6a	0.985	0.034	2.255	0.003	0.813	0.031	1.030	0.002
	transverse diameter of the middle of the diaphysis	F7a	0.970	0.034	1.765	0.002	DA	DA	DA	DA
	upper transverse diameter of the diaphysis	F7b	1.147	0.038	14.008	0.003	DA	DA	DA	DA
	upper sagittal diameter of the diaphysis	F7c	DA	DA	DA	DA	DA	DA	DA	DA
	lower transverse diameter of the diaphysis	F7d	1.164	0.033	2.744	0.002	1.877	0.075	17.110	0.065
	lower sagittal diameter of the diaphysis	F7e	DA	DA	DA	DA	DA	DA	DA	DA
	subtrochanteric transverse diameter of the diaph.	F9	1.045	0.031	2.104	0.002	1.250	0.041	2.331	0.002
	subtrochanteric sagittal diameter of the diaphysis	F10	DA	DA	DA	DA	0.889	0.034	1.333	0.002
	circumference of the middle of the diaphysis	F8	1.567	0.018	4.385	0.001	DA	DA	DA	DA
	upper width of the epiphysis	F13	2.364	0.023	8.955	0.001	DA	DA	DA	DA
	epicondylar width	F21	DA	DA	DA	DA	0.912	0.012	2.893	0.000
	vertical diameter of the head	F18	0.864	0.018	1.269	0.001	0.614	0.014	0.930	0.000
transverse diameter of the head	F19	0.864	0.018	1.277	0.001	0.397	0.009	0.441	0.000	
FIBULA	maximum length of the fibula	Fi1	2.559	0.007	13.243	0.000	2.296	0.007	8.408	0.000
TIBIA	overall length tibiae	T1	3.574	0.010	30.973	0.000	2.794	0.008	12.816	0.000
	medial length	T1b	3.957	0.011	37.410	0.000	2.966	0.009	13.420	0.000
	maximum width of the upper epiphysis	T3	1.217	0.016	2.554	0.000	1.364	0.020	4.184	0.001
	width of the lower epiphysis	T6	1.167	0.024	2.608	0.001	0.796	0.018	1.423	0.001
	minimum diameter of the middle of the diaphysis	T8	1.132	0.040	2.530	0.003	0.928	0.035	1.912	0.003
	width of the middle of the diaphysis	T9	1.000	0.044	1.972	0.004	0.765	0.035	1.458	0.003
	sagittal diameter in the upper foramen nutricium	T8a	1.235	0.037	2.873	0.003	0.957	0.032	1.910	0.002
	width of the diaphysis in the upper for. nutric.	T9a	0.863	0.034	1.445	0.002	0.629	0.028	1.001	0.002
	circumference of the middle of the diaphysis	T10	1.358	0.017	3.759	0.001	1.543	0.020	8.342	0.001
	circumference of the diaphysis on the for.nutric.	T10a	2.157	0.024	9.648	0.001	1.300	0.016	4.809	0.001
	minimum circumference of the diaphysis	T10b	1.170	0.016	3.059	0.001	1.099	0.016	3.311	0.001

of length. FA based on the size of the indicators (FA2, FA6) attains generally negligible or null values.

In order to establish whether cross asymmetry was present the individuals were divid-

Table 7. Absolute and relative frequencies of potentially right-handed (R) and left-handed (L) men and women, and of individuals showing no preference in the upper limbs (A).

	N	%		N	%
male R	95	81.2	female R	102	81.6
male L	14	12.0	female L	17	13.6
male A	8	6.8	female A	6	4.8
Total	117	100.0	Total	125	100.0

Table 8. Cross asymmetry evaluation. Absolute and relative frequencies of potentially right-handed (male R, female R) and left-handed (male L, female L) individual with longer bones of the right (R) or left (L) lower limbs, or with both bones the same length (A). N – number of individuals; F1 – maximum length of the femur; F2 – physiological length of the femur; T1 – overall length of the tibia; T1b – medial length of the tibia; Fi1 – maximum length of the fibula.

	male R		male L		female R		female L	
	N	%	N	%	N	%	N	%
F1 R	22	47.8	4	66.7	16	38.1	1	14.3
F1 L	18	39.1	1	16.7	19	45.2	3	42.9
F1 A	6	13.0	1	16.7	7	16.7	3	42.9
Total	46	100.0	6	100.0	42	100.0	7	100.0
F2 R	29	60.4	5	83.3	20	48.8	4	57.1
F2 L	15	31.3	0	0.0	15	36.6	2	28.6
F2 A	4	8.3	1	16.7	6	14.6	1	14.3
Total	48	100.0	6	100.0	41	100.0	7	100.0
T1 R	12	36.4	3	75.0	20	47.6	1	12.5
T1 L	19	57.6	1	25.0	16	38.1	5	62.5
T1 A	2	3.0	0	0.0	6	14.3	2	25.0
Total	33	100.0	4	100.0	42	100.0	8	100.0
T1b R	12	37.5	3	75.0	19	46.3	1	16.7
T1b L	19	59.4	1	25.0	18	43.9	3	50.0
T1b A	1	3.1	0	0.0	4	9.8	2	33.3
Total	32	100.0	4	100.0	41	100.0	6	100.0
Fi1 R	24	36.4	7	77.8	30	49.2	4	40.0
Fi1 L	30	45.5	2	22.2	21	34.4	6	60.0
Fi1 A	12	18.2	0	0.0	10	16.4	0	0.0
Total	66	100.0	9	100.0	61	100.0	10	100.0

ed by humerus length into those with a longer right humerus, those with a longer left humerus, and those in which both bones were the same length (Steele & Mays 1995, Čuk et al. 2001; Tab. 7). Testing was done in these groups to ascertain the asymmetry appearing in the bone lengths of the lower limbs (Tab. 8). The studied groups had, as expected, a similar percentage representation in the assemblage to the distribution of right- and left-handers and those showing no preference in modern European population. There were an insufficient number of individuals to demonstrate cross asymmetry, which requires paired bones from both limbs. In general, cross asymmetry was not recorded; it was found only among men with a longer right or left humerus, in the lengths of the tibia (57–59 %) and fibula (45.5 %).

DISCUSSION

In the bones of the upper limb bilateral asymmetry is in most cases directional (DA), while by contrast in the lower limb bilateral asymmetry is usually insignificant, ascribed to FA.

It is very important, particularly when studying FA, to remove or qualify the measurement error. In this study repeated measurements were applied only to 16 individuals (Steele & Mays 1995, Mays et al. 1999), and no measurement error was found. It is therefore adjudged that the established asymmetry is indeed a product of biological variability in the skeletal material studied. Nevertheless, for the study of FA measurements must be repeated several times for a large sample, and the measurement error, even if slight, must be estimated, in order that it not negatively influences the values of the size of FA. As Palmer (1994) has, for example, recommended, for a quantitative establishment it is appropriate to use, e.g. the FA10 index for a precise correction of the measurement error. For this reason, this study cannot be used to draw general conclusions regarding FA size, and thereby to directly evaluate the developmental stability and fitness of this sample of the population.

In the lower limbs FA was more common than DA, which confirms that there was no great asymmetric stressing, and that loads in general acted equally on both sides. As is true of earlier studies (e.g. Škvařilová 1999), the results of this study too confirm that in the bones of the upper limb it is possible to identify primarily DA (there are strong asymmetric loads). No differences between the sexes were recorded in FA size.

FA reached its greatest values in the length dimensions of bones and in the dimensions of the scapula, dependent on the indicator size (FA1, FA4). After removing the influence of the size of the given indicator (FA2 and FA6), FA size was shown to be negligible (in the order of thousandths values, often null). For comparison, Škvařilová (1999), for example, found FA in the forearm length and the breadth of the lower epiphysis of the humerus in clinical material; such results were not however obtained in this study. Further comparisons with the literature were not possible, as no other FA studies using the same statistical approach could be found.

The DA study results (Fig. 3) accord with the results presented in several publications, as the DA of the upper limbs trends in a vast majority of cases to the right, while in the lower limbs it favours the left side (Škvařilová 1999, Čuk et al. 2001). Schell et al. (1985) also recorded right side asymmetry among the upper limbs of adolescents, but do not confirm DA in the lower limbs (although according to many studies asymmetry generally increases with age: Steele & Mays 1995). Similarly, the present study confirms that DA does not appear in the lower limbs as often as it does in the upper (Steele & Mays 1995, Škvařilová 1999, Čuk et al. 2001).

In this assemblage DA is very frequent in the dimensions of the upper limbs, appearing on all bones. The most asymmetrically loaded bone is the humerus (the right humerus is longer and more robust), with all its dimensions being directionally asymmetrical. Moreover, the division of individuals by humerus length really does reflect distribution of handedness in modern European population (Annett & Kilshaw 1983). This leads the authors to conclude that in the humerus in particular, but also in the bones of the forearm (where the right is longer and more robust), asymmetric load during power tasks is the main cause of DA. This is supported by the conclusions of several other studies: foetuses generally have an even longer left humerus (but generally suck the right thumb), juveniles generally have a longer right humerus and ulna, while adolescents almost always have longer right upper limb. Evidently, then, DA develops post-natally, and in children in particular increased with age and with long-term loads (Hepper et al. 1991, Steele & Mays 1995, Škvařilová 1999). It is therefore possible that the individuals in the "Pachner Collection" were heavily loaded on one (dominant) upper limb. The presumption stemming from the study of, for example, Čuk et al. (2001), that the proximal epiphysis of the

humerus is more asymmetrical than the distal epiphysis, could not be confirmed. It is not, therefore, possible to state that the shoulder section is more asymmetrically mechanically loaded than the elbow.

It should not be forgotten that asymmetry can also be conditioned by such non-specific loads as unsuitable living conditions and lack of nourishment (Livshits & Kobylansky 1987, Graham et al. 1993). It is necessary to bear such environmental stress in mind in this series, too, given the poor social standing of the individuals concerned (Pachner 1937).

It follows from earlier studies (e.g. Huggare & Houghton 1995, Mays et al. 1999), that the right clavicle is shorter and more robust in a majority of individuals; this study accords with such conclusions. This phenomenon is explained by the assumption that the growth of the clavicle of the dominant limb is suppressed thanks to greater muscular development (connected with hand preference) in this area (Mays et al. 1999).

In the lower limbs DA appears less often than FA, in almost all cases trends to the left, so that the dimension of the left side is significantly greater than that of the right side. In this collection, DA was recorded in the lower limbs in a small number of femur diaphyses, but not in the tibia or fibula. In this collection asymmetry appeared more obviously in the dimensional measurements of the bone diaphysis than in the lengths. The authors agree with Čuk et al. (2001) that this arises from the fact that the length growth of the bone finishes in adulthood, while the width increases under biomechanical influences throughout life.

In this assemblage the femur is longer on the left side. In comparing this result with those published elsewhere, conclusions as to the occurrence of asymmetry in femur length are diverse. Velemínský (2000) has recorded DA in the femur length of males favouring the right side, while Latimer & Lowrance (1965) and Singh (1970) confirm a heavier lower left limb, but found no asymmetry in the bone length; similarly, Ruff (1992) could not confirm differences in femur length. The results of the present study accord with those of Čuk et al. (2001), where DA was found to favour a longer left femur. The more massive diaphyses found in the femurs of both sexes by this study are confirmed by other studies, such as those by Ruff & Hayes (1983), Macho (1991), Čuk et al. (2001) and Velemínský (2000). The authors suppose that the reason for this is the main, supportive function of the lower left limb regardless of handedness. In terms of shape, men have the left femur with less anteroposterior flattening than the right. Similarly a more rounded diaphysis of the right femur was found by Macho (1991). The women in this modern assemblage are more asymmetrical in the lower limb than the men; it is therefore impossible to confirm the assumption that a lower degree of asymmetry will occur among women because of their certain genetic resistance to environmental stress (Schell et al. 1985, Lazenby 2002). A similar conclusion was reached by Ruff & Hayes (1983) and by Stránská et al. (2002), who found greater asymmetry in the femur shank among women. In contrast, Velemínský (2000) found asymmetry in the lower limbs to favour men more often.

The dimensions of the epiphysis are greater on the right side. This has been explained in a number of publications by the greater load placed on the knee (and hip) of the “non-supportive leg”, used for special functions. Macho (1991) has also reported DA in the dimensions of the upper epiphysis in women.

In the present modern assemblage neither the tibia nor the fibula display DA. Insignificant differences are confirmed in men by a longer and more robust left tibia, similarly as in the studies of Čuk et al. (2001) and Velemínský (2000). The authors suppose that

a more developed left tibia is an expression of the dominance of the left lower limb (given handedness, the reverse of the upper limbs). Women have in the insignificant differences more robust and longer the right tibia, in contrast to the men.

In terms of sexual dimorphism in the occurrence of asymmetry, studies to date have come to contradictory conclusions. Some authors have not found differences between the sexes (Steele & Mays 1995, Škvařilová 1999, Plochocki 2002), while others believe that this is a factor contributing to asymmetry (e.g. Schultz 1937). The results of this study do show a difference in asymmetry between the sexes; women appeared to be more asymmetrical (in 81 % of the upper limb dimensions and 47 % of the lower limb dimensions). Greater asymmetry among women has also been described in a study by Ruff & Hayes (1983). The authors, like Ruff (1992), found no differences between the sexes in the asymmetry of the dimensions of length.

From the results of the paired t-test it is apparent that the DA of the upper limbs always trends towards the right, while the DA of the lower limbs generally trends to the left. Such results may indicate the presence of cross asymmetry. To establish cross asymmetry the lengths of the long bones of the upper and lower limbs were compared. Generally, it has been found that right-handers have a better developed right upper limb and, with this, left lower limb (Ingelmark 1946, Siniarska & Sarna 1980, Ruff & Jones 1981), the greatest length of the humerus was therefore used to divide the sample into hypothetical right-handers (with a longer right humerus) and left-handers (with a longer left humerus), after, e.g., Steele & Mays (1995) and Čuk et al. (2001).

The studied assemblage was observed to have a similar percentage representation of individuals with a longer right (81 %) or left (12–13 %) humerus, or both the same length (5–7 %) as in the modern population according to previous studies (e.g. Annett & Kilshaw 1983: 82 % right-handers, 15 % left-handers, 3 % with no preference; Steele & Mays 1995: 81 % right-handers, 16 % left-handers, 3 % with no preference).

Cross asymmetry was tested for in the tibia, as was the presumption that the femur would be longer on the left side regardless of handedness (the supportive leg; Čuk et al. 2001). In the assemblage used for the present study cross asymmetry was found only among men (both the hypothetically right-handed and left-handed), in the lengths of the tibia and fibula. A possible explanation of this might be the fact that men were more likely to come under hard physical loads than women; further interpretations within other “groups” are not possible, given the insufficiently large numbers of individuals concerned. The supportive function of the left lower limb regardless of handedness is expressed in the significant left-right differences in the femur; in the individual groups, however, this assumption could not directly be affirmed.

CONCLUSIONS

This study has considered fluctuating, directional and cross asymmetry as well as antisymmetry in the human skeleton. The investigated material comprised an identified, osteological collection dating to the 1930s. A total of 157 adult female and 143 adult male postcranial skeletons were measured, with 21 metric characteristics of the bones of the upper limbs (the humerus, radius, ulna, clavicle and scapula) and 27 metric characteristics of the bones of the lower limbs (the femur, tibia and fibula) being recorded. The results obtained may be summarised into the following points:

Antisymmetry was not found in any of the studied indicators.

The presence of DA was noted in particular in the upper limb, while in the lower limb

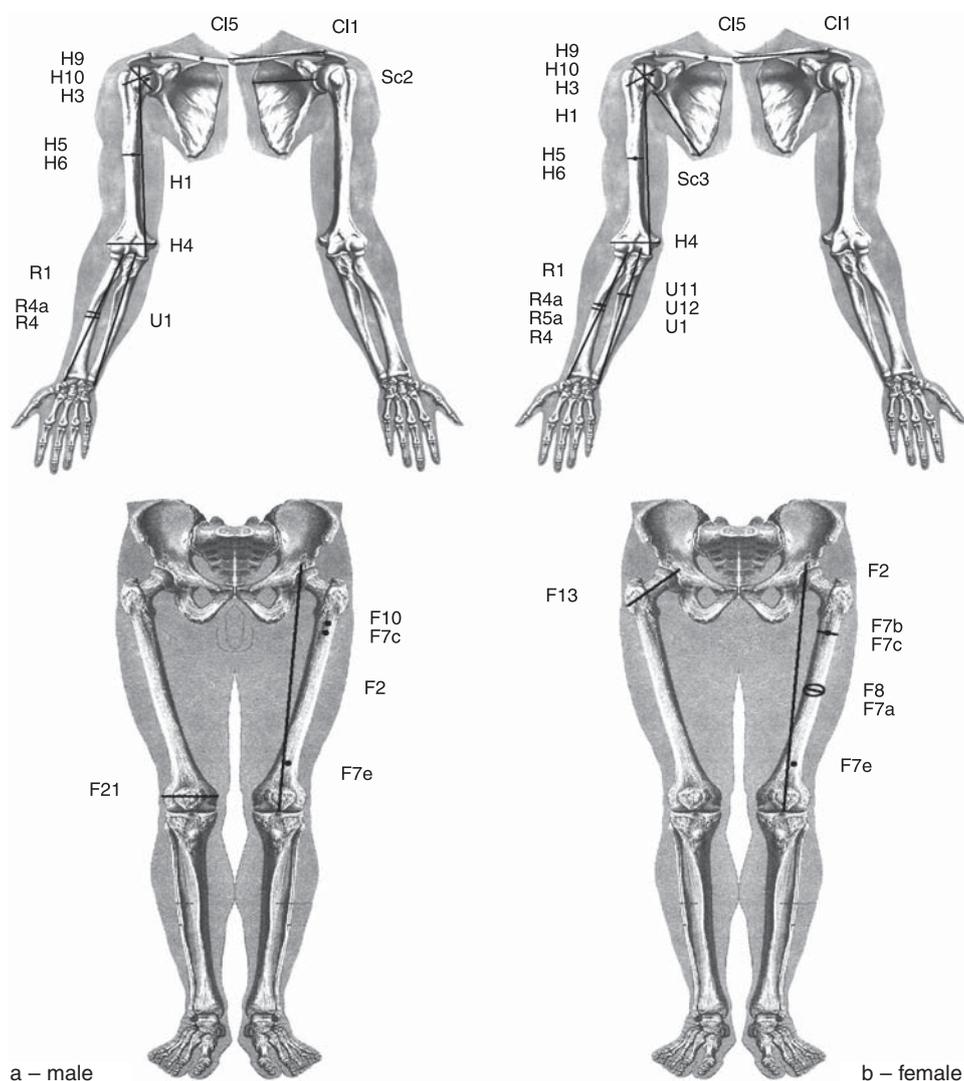


Fig. 3. Depiction of the dimensions in which directional asymmetry was observed.

FA was apparent in most of the dimensions, albeit at very low values. This may be explained by the more asymmetric use of the upper limbs as opposed to the lower, the load on which comes in particular from “symmetrical” walking.

The most asymmetric bone is the humerus, probably reflecting a hand preference. DA was recorded in all of the dimensions of the humerus, always favouring the right side. The proportion of individuals divided according to humerus length matches the division of right-handers, left-handers and those displaying no preference in the modern population. Similarly, the forearm bones also display (especially in their dimensions of length) a tendency to favour the right side expressed in DA. It is therefore likely that DA in the long bones of the upper limbs reflects the handedness of the individuals concerned. Skeletal asymmetry thus seems resistant to cultural pressures to “correct” handedness.

The clavicle is more robust on the right side, but shorter. At this point it is possible to seek out a correlation with suppressed growth of the clavicle to its length on the side on the dominant limb due to the greater development of the muscles in this area.

DA is more frequent in the upper limbs than in the lower. In the lower limbs it was found only in the femur, in most cases favouring the left side. DA appeared more often among women than among men.

Cross asymmetry in the tibia was found only among men, and probably expresses the dominance of the opposite lower limb to that of the preferred upper limb. The supportive function of the lower left limb is expressed in the strong DA of the femur, regardless of handedness.

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Příloha B

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Variability of the Upper Palaeolithic skulls from Předmostí near Přerov (Czech Republic): Craniometric comparison with recent human standards

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Abstract

One of the largest skeletal series of the Upper Palaeolithic period from Předmostí was destroyed during the Second World War, but the study of this material continues up to the present. The discovery of Matiegka's original photographic documentation on glass plates [Velemínská et al., 2004. The use of recently re-discovered glass plate photo-documentation of those human fossil finds from Předmostí u Přerova destroyed during World War II. *J. Nat. Mus. Nat. Hist. Ser.* 173, 129–132] gives an opportunity to perform a new and detailed craniometric analysis of five adult skulls in their lateral projection.

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The craniometric data were analysed using specialised Craniometrics software, and the analysis included morphological and dimensional comparisons with current Central European norms. The aim of the study was not only to monitor the skull shape as a whole, but predominantly, to evaluate the size and shape of various parts of the splanchnocranium.

The Upper Palaeolithic skulls are significantly longer, and male skulls are also higher than the current norms. The crania of anatomically modern humans are characterised by two general structural features: mid-lower facial retraction and neurocranial globularity. The height of the face of the Palaeolithic skulls corresponds to that of the current Central European population. The face has a markedly longer mandibular body (3–4 SD), while female mandibular rami are shorter. The skulls are further characterised by a smaller gonial angle, the increased steepness of the mandibular ramus, and the greater angle of the chin. These changes in the size and shape associated with anterior rotation of the face produce a strong protrusion of both jaws, but the sagittal inter-maxillary relationships remain unchanged. The observed facial morphology is similar to the Czech Upper Palaeolithic skulls from Dolní Věstonice.

This study confirms the main diachronic changes between skulls of Upper Palaeolithic and present-day human populations.

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Introduction

The fossil bone remains of almost 30 skeletons from Předmostí near Přerov are among the most important finds of anatomically modern humans in the world (Ferrie, 1997; Smith, 1997). Some of the fossils were discovered by Jindřich Wankel, Karel J. Maška, Jan Knies and Martin Kříž as early as the second-half of the 19th century, and the others were found by Karel Absolon and J. Skutil (Vlček, 1996) in the first-half of the 20th century. Their estimated age is 25,000–27,000 years (Svoboda, 2001).

The sample from Předmostí has drawn much attention since its discovery because, due to certain morphological characteristics, it was regarded as belonging to a less advanced type of modern human than the Cro-Magnon. It was generally held by scholars that members of this population bridged the gap between Neandertals and recent Europeans (Smith, 1997). The reasons for the morphological similarities or the archaic nature of certain characteristics of the Central European Gravettian fossils serve as an argument for the multi-regional model of evolution (Wolpoff, 1999) and, are also discussed as “evidence that supports some degree of prior admixture with regional Neandertal populations” (Trinkaus and Svoboda, 2006).

Following the destruction of most of the fossils as a result of a fire at the Mikulov Castle at the end of the Second World War in 1945, the only sources of information on the human fossil finds at Předmostí are the two-part monograph by Matiegka (1934, 1938) and several casts (Jelínek and Orvanová, 1999). The recent discovery of the photographic documentation on glass negatives of a series of skeletal remains from Předmostí (Velemínská et al., 2004) at least partially compensates for the loss of the original skeletons.

Morphometric data on the Upper Palaeolithic series from Předmostí are still used as comparative material in palaeoanthropology; for example, they are used for assessing facial proportions and their changes between the Neanderthals and anatomically modern human (Trinkaus, 2003), and for studying cranial shape development in the European population (Brace et al., 2006). In some studies, where cranial morphology of the Neanderthals is compared with those of other groups, up to a half of the material from the European Upper Palaeolithic (EUP) period comes from Předmostí (e.g. Harvati et al., 2004; Thackeray et al., 2005).

It is generally acknowledged that cranial size and shape are strongly controlled by genetic mechanisms (Manfredi et al., 1997; Johannsdottir et al., 2005). Therefore, the study of cranial size and shape can yield information on intra-population variability and possible family connections within the group, as was indicated in the case of the individuals from Palaeolithic Dolní Věstonice (Alt et al., 1997).

The purpose of this study is to monitor diachronic variability in the size and shape of skulls within the territory of Central Europe since the Upper Palaeolithic until today. We have posed the question whether we can prove, using selected methods, that the most typical evolutionary changes of *Homo sapiens* are the development of neurocranial globularity and decreased facial convexity (Lieberman et al., 2002). Our argument is based on detailed craniometric analysis of the photographs of Předmostí adult skulls in the lateral projection, with special emphasis on facial morphology and a comparison with recent human standards.

Skulls from Předmostí are compared with the craniometric variability of recent males and females and with the variability of individuals from Dolní Věstonice (Vlček and Šmahel, 2002; Trinkaus and Svoboda, 2006). All samples used in this study derive from the same geographic area of Moravia. The fossil samples belong to the Pavlovian cultural group, the central European form of the Gravettian culture of Upper Palaeolithic Europe. The standard information acquired was supplemented by certain measurements and angles not commonly taken in the first-half of the last century (see e.g. Bernhard et al., 2002). Although lateral radiographs have only been used relatively recently in palaeoanthropology (Argyropoulos et al., 1989; Vlček and Šmahel, 2002; Kuroe et al., 2004; Cuzzo, 2005), this technique can offer important information; for example, for assessing changes in cranial shape in relation to the expansion of the brain during the course of evolution (e.g. Ross et al., 2004), and for assessing the facial morphology of an individual from the skull.

Materials

Craniometric photographs of five adult fossil skulls from Předmostí (male skulls P1, P3, P9, female skulls P4, P10) were evaluated. The sex of the fossils was previously estimated by several researchers (Matiegka, 1934; Šefčáková et al., 2003; Katina et al., 2004). Despite the existence of certain discrepancies between sex determination according to the skulls and the pelvises of some individuals from

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Předmostí (Brůžek et al., 2008), the sex of the skulls in this study remains the same as determined by Matiegka (1934).

Craniometric data of Předmostí were compared with norms based on lateral radiographs of 52 healthy males and 36 females from the archive of the Clinic of Plastic and Reconstructive Surgery, 3rd Faculty of Medicine, Charles University in Prague. All adults represented a randomly selected group of volunteers from among students and patients hospitalised with minor trauma at the Departments of surgery and plastic surgery of Charles University Faculty of Medicine. The first group included 52 men of average age 28 years and 10 months and their radiographs were taken in the mid-1970s. The second group included 36 women of average age 20 years and 4 months and was compiled from radiographs taken in the mid-1990s. Photographs and images only of healthy Czech individuals who had no obvious shape disharmony, had clinically acceptable occlusion and no prior orthodontic treatment have been used. Cases of congenital anomalies were excluded.

In order to expand the sample of Czech Upper Palaeolithic skulls, to the original group of five we added radiographs from Vlček and Šmahel (2002). As in the case of the previous group, we also based our work on the measurement of lateral radiographs. For comparison, we used metric data of male skulls from Dolní Věstonice (DV 13, 14, 16). The young adult, Dolní Věstonice 15, who suffered serious congenital developmental malformations (Trinkaus et al., 2001), was not included in the study. The DV3 skull has not been evaluated since it also showed traumatic damage to the right side of the face and there were no images of this skull.

Methods

The glass negatives of fossil skulls were digitised using special software (RGB 360 dpi at 30 cm, implementation by a Rollei scanning screen and SilverFast 6.0 software). Twenty x , y coordinates of key craniometric landmarks were obtained by using SigmaScan software, which created basic data entry for the special Craniometric software (Fig. 1). This technique is currently used in orthodontics, clinical anthropology, osteology and even palaeoanthropology for measuring lateral radiographs. As the photographs of fossils were taken in the 1930s, we could not ensure stable conditions during exposure. It is very important to preserve the insertion of mandibles into the TM joints and articulation of the teeth. The fact that the position of the mandibles was not always entirely correct (see Figs. 2 and 3) has been the reason why the dental relations were not evaluated. Testing the reliability of photograph measurements was the first prerequisite for the subsequent metric analysis. The coefficient of reliability was between 0.87 and 0.97, the systematic error was significant at the lowest level of significance ($\alpha = 0.05$) in only one dimension (Nasion-Mentale), and occurred randomly (Velemínská et al., 2003).

It is important to stress that our study is based on the comparison of dimensions acquired by different techniques – via measurements of photographs and radiographs. The application of both techniques is common in forensic anthropology in

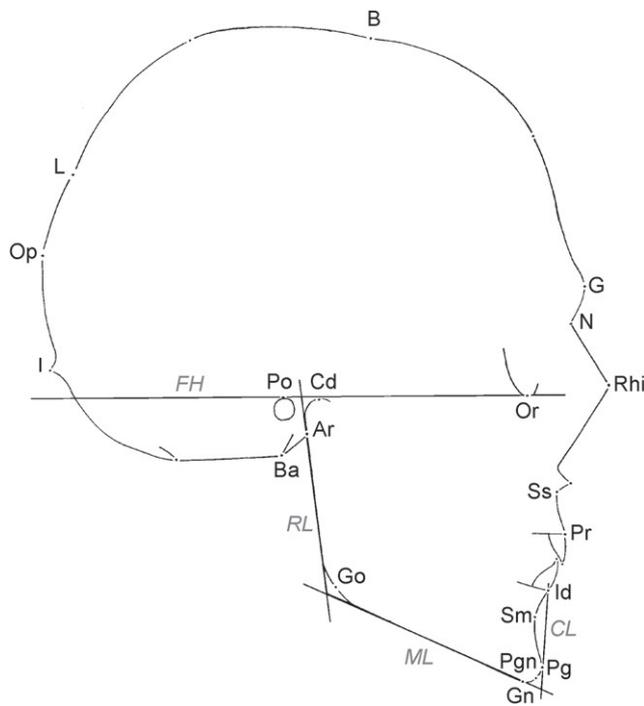


Fig. 1. Cephalometric points (landmarks) and reference lines used in this study: Ar (articulare) – intersection of inferior contour of the posterior cranial base and posterior contour of the ramus; B (bregma) – intersection of the coronal and sagittal sutures; Ba (basion) – most posteroinferior point on the clivus; Cd (condyion) – most superior point on the condylar head; G (glabella) – the most anterior point on the arcus superciliaris; Gn (gnathion) – the lowest point of the mandibular symphysis; Go (gonion) – point on the angle of the mandible determined by the axis of ML/RL angle; I (inion) – top of the protuberantia occipitalis externa; Id (infradentale) – point of the alveolar contact with the lower central incisor; L (lambda) – intersection of the sagittal and lambda sutures; N (nasion) – the most anterior point on the frontonasal suture; Op (opistocranium) – point on the surface of the cranial vault farthest from the glabella point; Or (orbitale) – the lowest point on the orbital margin; Pg (pogonion) – the most anterior point on the bony chin; Pgn (prognathion) – point on the mandibular symphysis farthest from Cd; Po (porion) – the most superior point on the porus acusticus externus; Pr (prosthion) – point of alveolar contact with the upper central incisor; Rhi (rhinion) – the most anteroinferior point on the nasal bone; Sm (supramentale) – the deepest point on the anterior contour of the mandibular symphysis; Ss (subspinale) – the deepest point of the subspinal concavity; CL – the line through Pg and Id; FH – the line through Or and Po points; ML – tangent to the mandibular body through Gn; RL – tangent to the mandibular ramus through Ar.

super-projection methods, or in research into historical personalities (Vlček and Šmahel, 1998). Metric evaluation of skull photographs is considered acceptable (Benson and Richmond, 1997), although errors of this method are likely to be

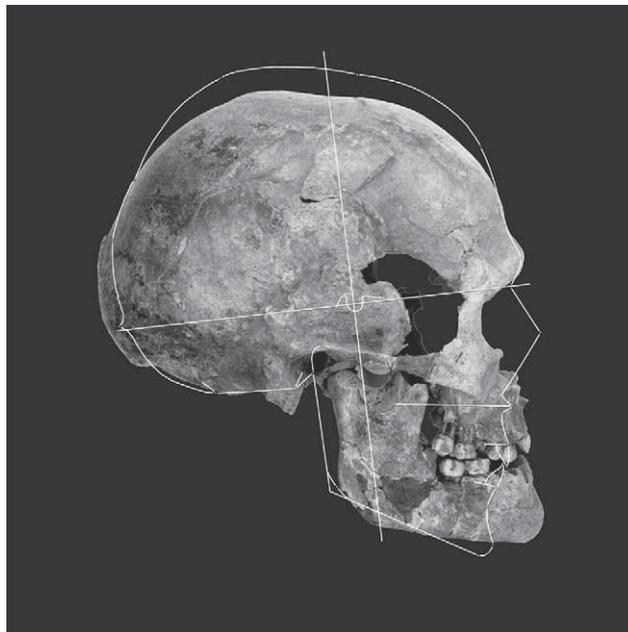


Fig. 2. Illustration of the size and shape differences between a fossil (photograph of skull P1) and a recent (male craniogram) skull.

greater than those due to digitisation of radiographs. Comparison of dimensions from photographs and radiographs of the same series of skulls (Hudcová, 2006) demonstrated that in five of six linear dimensions also analysed in this study (G–Op, G–L, B–L, N–B, N–Pr), the confidence coefficient of measurements was between 0.95 and 0.90. The lowest value of the confidence coefficient (0.84) was in the case of the N–Rhi dimension.

The use of photographs represents another difficulty of the method: the lack of information regarding the conditions under which photographs of the Předmostí skulls were taken (magnification, focal length, or type of camera). We resolved this difficulty by not relying on truly measured variables, but by using the *z*-score values. Thus, while there are some technical difficulties in combining and comparing data derived from radiographs and photographs, overall the procedure seems to be reliable (Benson and Richmond, 1997).

The Craniometrics software was used for detailed craniofacial metric analysis of lateral radiographs or photographs. The (N–B) value (Matiegka, 1934) was chosen as the scale for measuring skull photographs.

We evaluated 30 linear or angular (shape) variables. Size dimensions were marked as two points (G–Op), angular characteristics as three points (N–B–L) or two line intersections (ML/RL). B–NL is the perpendicular distance from bregma (B) to the connecting line NL. Nine characteristics were located on the neurocranium (G–Op, G–L, B–L, N–B, L–Ba, B–Ba, B–NL, N–B–L, N–I–L) and with exception of three of

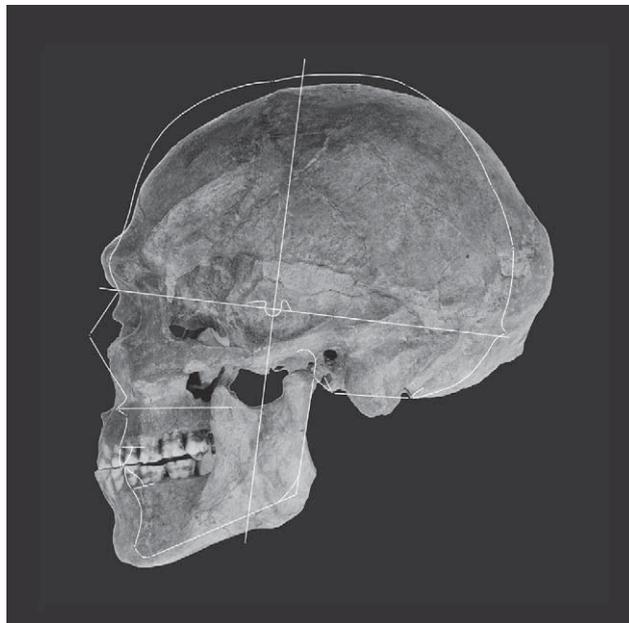


Fig. 3. Illustration of the size and shape differences between a fossil (photograph of skull P3) and a recent (male craniogram) skull.

these (B–NL, N–B–L, N–I–L), they were measured directly on the skulls by Matiegka (1934).

In the splanchnocranium, we analysed nine size variables (N–Rhi, N–Pr, N–Gn, Id–Gn, Pgn–Go, Cd–Go, Ss–Ar, Sm–Ar and Pgn–Ar) and 12 shape variables (Ss–N–Sm, Pr–N–Id, N–Ss–Pr, ML/RL, ML/FH, RL/FH, CL/ML, Ar–N–Ss, Ar–N–Sm, Ar–N–Pg, N–Ar/RL and N–Ar/ML). All characteristics were compared with the recent norm, and ten characteristics were chosen for comparison with similar craniometrics of Upper Palaeolithic skulls from Dolní Věstonice (Vlček and Šmahel, 2002).

The recent Czech osteological standards were created using recent radiographs (Macková, 2004). Attention was paid to the different preservation (completeness) of skulls and to the measurement availability on photographs. Shape characteristics were related to the nasion-articulare distance (N–Ar). Similar dimensions can be also expressed in relation to the Frankfurt horizontal line (FH). These two lines made it possible to measure shape variables on photographs where the sella, an important craniometric point, was missing. Some of these lateral radiographs (35 females and 36 males) were used for the construction of mean male and female craniograms (Šmahel et al., 1998). These were used for the comparison of modern Czechs reference samples with Předmostí 1, 3, 4, 9 and 10 (Figs. 2–6).

Average values and standard deviations (SD) of the dimensions of the recent population have been used to calculate the *z*-score. The *z*-score is the distance in SD

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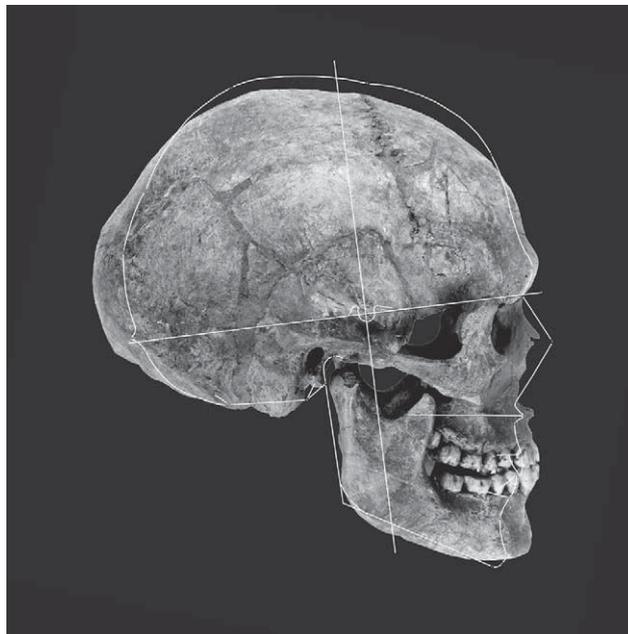


Fig. 4. Illustration of the size and shape differences between a fossil (photograph of skull P9) and a recent (male craniogram) skull.

of a measurement or an individual value of a Předmostí skull from the mean of the reference sample (standard). A fossil deviation of minimally two SDs from this mean is considered as significant. The calculations are accompanied by plots, where the zero axis represents the average of recent male and female skulls, the highlighted points represent the magnitude of the z -score.

Similarity (or dissimilarity) of the skull shape in Předmostí versus recent samples was evaluated using the multivariate method of cluster analysis. The mutually similar skulls were clustered on the basis of Euclidean distance. To determine the distance among objects in a cluster, three methods of joining the cluster tree were used: single linkage, complete linkage and Ward's method. The calculations and graphs were done using MS Excel 2003 and Statistica 6.0 statistical software packages.

Results

The lists of assessed linear and shape variables are presented in Tables 1–3, supplemented for each skull by the SD from the mean value in the sample of skulls from the recent population expressed as a magnitude of SD (z -score). In Tables 1

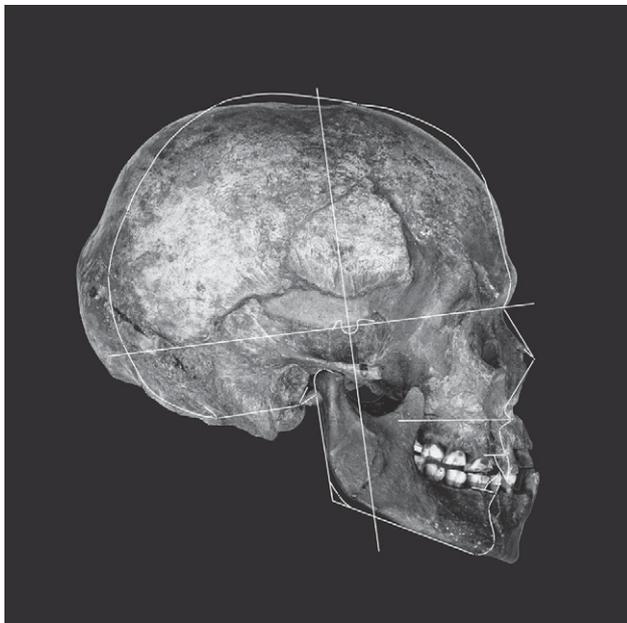


Fig. 5. Illustration of the size and shape differences between a fossil (photograph of skull P4) and a recent (female craniogram) skull.



Fig. 6. Illustration of the size and shape differences between a fossil (photograph of skull P10) and a recent (female craniogram) skull.

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Table 1. Size and shape variables of male Upper Palaeolithic skulls from Předmostí, recent standard (mean, SD), and *z*-score (bold marked values over ± 2 SD)

variable	Mean (recent)	SD (recent)	P1	<i>z</i> -score	P3	<i>z</i> -score	P9	<i>z</i> -score
G–Op	180.559	4.921	189.000	1.715	201.500	4.256	196.000	3.138
G–L	173.790	4.696	183.000	1.961	193.000	4.091	187.000	2.813
B–L	109.826	5.748	125.000	2.640	120.000	1.770	120.000	1.770
N–B	114.404	5.150	107.000	–1.438	120.000	1.087	115.000	0.116
L–Ba	115.308	4.872			116.000	0.142	116.000	0.142
B–Ba	140.312	4.935			133.000	–1.482	134.000	–1.279
B–NL	71.657	4.849	71.412	–0.051	73.022	0.281	74.895	0.668
N–B–L	100.387	3.633	103.000	0.719	105.160	1.313	102.253	0.513
N–I–L	77.252	3.810	87.801	2.769	80.852	0.945	83.680	1.687
N–Rhi	23.078	3.599					19.638	–0.956
N–Pr	69.855	3.991			78.757	2.230	68.673	–0.296
N–Gn	120.281	6.704			131.365	1.653	117.855	–0.362
Id–Gn	32.193	2.883	31.716	–0.166	43.133	3.794	31.638	–0.193
Ss–Ar	85.582	4.090			102.116	4.042	96.792	2.741
Sm–Ar	96.741	4.375			112.824	3.676	111.049	3.270
Pgn–Ar	111.041	4.782			125.166	2.954	124.888	2.896
Ar–N–Ss	62.933	3.432			71.770	2.575	74.816	3.462
Ar–N–Sm	60.644	3.354			66.752	1.821	71.704	3.298
Pgn–Go	73.311	3.802	83.172	2.593	90.180	4.436	87.808	3.812
Cd–Go	61.619	4.118	61.631	0.003	65.505	0.944	65.741	1.001
ML/RL	121.772	7.001	101.870	– 2.843	105.430	– 2.334	109.640	–1.733
CL/ML	70.943	5.926	68.350	–0.438	89.450	3.123	72.080	0.192
ML/FH	21.655	6.782	6.230	– 2.274	18.330	–0.490	13.840	–1.152
RL/FH	79.894	4.318	84.400	1.044	92.990	3.033	84.170	0.990
N–Ar/ML	47.458	7.111			40.530	–0.970	34.760	–1.790
N–Ar/RL	105.707	4.612			115.460	2.110	105.260	–0.100
Ss–N–Sm	2.353	2.161			5.019	1.234	3.112	0.351
Pr–N–Id	2.741	1.408			1.200	–1.094	2.732	–0.007
N–Ss–Pg	178.587	5.006			168.138	– 2.087	176.742	–0.369

and 2, bold letters indicate the *z*-score values of those dimensions whose magnitude is at least 2 SD. The 95% of the *z*-score values lie within the ± 2 SD interval (normal, Gaussian distribution).

The size and shape differences of the fossil skulls with regard to recent standards are also illustrated in Figs. 7–9.

The individual evaluation of fossil skulls is presented as compared to the recent population (modern standard) represented by a recent Czech reference sample, then, the generalised evaluation follows in subsequent paragraphs. The determined size and shape properties of the skulls from Předmostí are then compared to the fossil skulls from Dolní Věstonice.

Table 2. Size and shape variables of female Upper Palaeolithic skulls from Předmostí, recent standard (mean, SD), and *z*-score (bold marked values over ± 2 SD)

variable	Mean (recent)	SD (recent)	P4	<i>z</i> -score	P10	<i>z</i> -score
G–Op	173.982	173.982	191.500	2.129	185.500	1.400
G–L	168.829	8.460	185.000	1.912	175.000	0.729
B–L	111.906	7.656	120.000	1.057	107.000	–0.641
N–B	108.685	4.825	114.000	1.102	112.000	0.687
L–Ba	112.357	6.285	121.000	1.375		
Ba–B	134.924	5.128	136.000	0.210		
B–NL	71.277	4.893	73.882	0.532	69.510	–0.361
N–B–L	99.201	4.194	101.308	0.502	103.689	1.070
N–I–L	81.253	3.537	85.780	1.280	82.705	0.411
N–Rhi	23.025	4.074	21.005	–0.496	16.371	–1.633
N–Pr	64.794	4.674	62.194	–0.556	62.867	–0.412
N–Gn	109.785	7.627	111.461	0.220	107.142	–0.346
Id–Gn	28.476	2.860	30.803	0.814	26.617	–0.650
Ss–Ar	80.554	80.554	86.588	1.628	90.514	2.687
Sm–Ar	89.988	89.988	102.445	2.948	100.879	2.577
Pgn–Ar	101.909	4.806	109.378	1.554	109.825	1.647
Ar–N–Ss	62.731	2.906	73.013	3.538	72.971	3.524
Ar–N–Sm	60.625	3.047	68.914	2.720	68.082	2.447
Pgn–Go	70.034	3.619	86.142	4.451	82.975	3.576
Cd–Go	55.240	4.787	47.010	–1.719	51.636	–0.753
ML/RL	120.134	6.938	115.690	–0.641	112.800	–1.057
CL/ML	71.238	6.479	83.930	1.959	76.490	0.811
ML/FH	21.484	6.921	21.560	0.011	14.900	–0.951
RL/FH	81.351	4.142	85.990	1.120	82.250	0.217
Ss–N–Sm	2.106	2.182	4.099	0.913	4.889	1.276
Pr–N–Id	3.426	1.745	2.243	–0.678	5.493	1.184
N–Ss–Pg	179.077	5.819	168.318	–1.849	171.275	–1.341

Předmostí skull 1 (P1)

The male skull, P1, is the least well preserved of all the five studied skulls. As a significant section of the skull base and the skeleton of the upper face are missing, we limited our evaluation to the section of the cranial vault and the lower jaw (Table 1, Figs. 7–9). The overall shape of the skull in the lateral view and its differences compared to the average of the recent population are depicted only in Fig. 2.

The cranium of P1 is longer by 1.7 SD than the average of the recent population. This difference is mostly due to the significantly longer B–L chord (2.6 SD), while the N–B chord is shorter compared to the recent population (–1.4 SD). Another chord, B–L concurrently influences the angle N–I–L, which is larger by 10° compared to the recent population (2.8 SD). On the basis of the photograph in Fig. 2, the cranium

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Table 3. Shape and size variables of male Upper Palaeolithic skulls from Dolní Věstonice, recent standard (mean, SD), and *z*-score values

Variable	Mean (recent)	SD	DV13	<i>z</i> -score	DV14	<i>z</i> -score	DV16	<i>z</i> -score
G–Op	180.559	4.921	198.000	3.544	187.000	1.309	203.000	4.560
Ba–B	140.312	4.935	131.000	–1.887	134.000	–1.279	137.000	–0.671
Ar–N–Ss	62.933	3.466	79.500	4.780	64.500	0.452	72.500	2.760
Ar–N–Sm	60.644	3.386	71.000	3.058	62.500	0.548	69.000	2.468
Ar–N–Pg	62.314	3.488	72.000	2.777	63.000	0.197	71.000	2.490
ML/RL	121.772	7.069	113.500	–1.170	110.000	–1.665	113.000	–1.241
N–Ar/ML	47.458	7.111	41.000	–0.908	44.500	–0.416	37.000	–1.471
N–Ar/RL	105.707	4.612	108.000	0.497	115.000	2.015	104.000	–0.370
Ss–N–Sm	2.353	2.182	8.500	2.817	2.000	–0.162	3.500	0.526
N–Ss–Pg	178.587	5.055	163.500	–2.985	176.500	–0.413	176.000	–0.512

appears significantly lower. This information cannot be evaluated metrically in view of the absence of the skull base.

The mandible of P1 differs from the recent population with its markedly longer body, while the length of its ramus corresponds to the average of the reference population. The mandibular angle and the inclination of the body with respect to the Frankfurt horizontal are significantly smaller, which is documented not only by the graph but also by Fig. 2. The question remains, whether the markedly different position of the mandible with respect to the Frankfurt horizontal is not the consequence of maxillary reconstruction.

Předmostí skull 3 (P3)

The very well preserved male skull P3 enables the evaluation of all the studied variables, with the exception of the length of the nasal bones (N–Rhi) (Table 1, Figs. 3 and 7–9).

Compared to the recent population, the neurocranium of P3 is markedly longer (4.3 SD) and at the same time lower (–1.5 SD). The length of the skull is affected, to a great extent, by the vaulted section of the glabella and the length of the parietal bone (G–L), and less so by the frontal bone chords (N–B). The cranial angular dimensions show no significant shape differences, compared to the recent population.

The height dimensions of the splanchnocranium are greater than in the recent population. The smallest difference is noted for the total height of the face (1.7 SD), while more marked differences are noted in the partial height dimensions of the upper (3.8 SD) and lower (4.4 SD) face, which are affected by the strong protrusion of both jaws. The protrusion itself is best characterised by the great differences expressed with the aid of the linear dimensions Ss–Ar, Sm–Ar and the angles

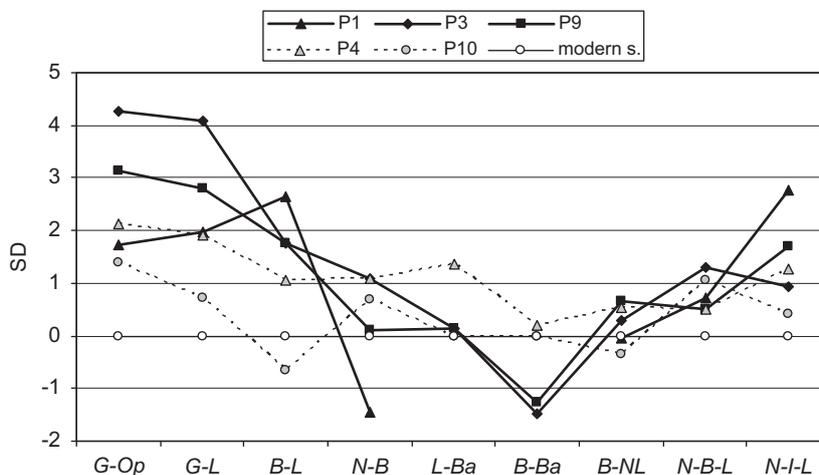


Fig. 7. Plot of the size and shape differences of the neurocranium in the Předmostí fossil skulls sample in relation to the recent reference sample using z -score.

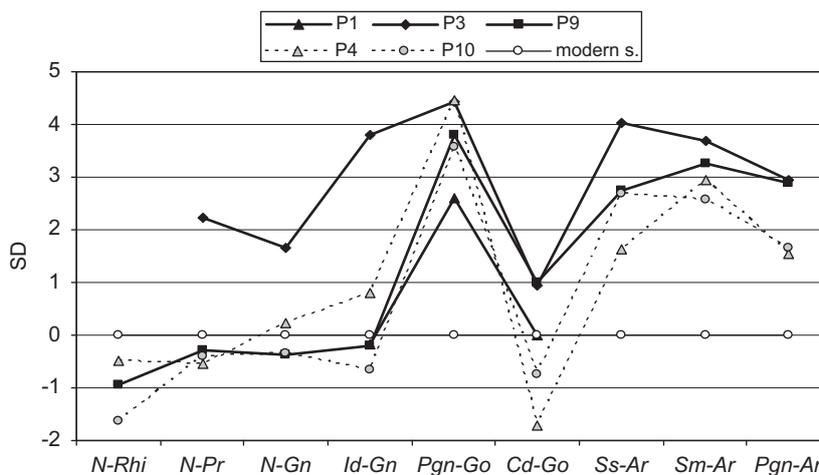


Fig. 8. Plot of the size differences of the splanchnocranium in the Předmostí fossil skulls sample in relation to the recent reference sample using z -score.

Ar–N–Ss, Ar–N–Sm. The skull has a typically large convexity of the face, N–Ss–Pg (–2.1 SD)

The lower jaw of P3 significantly differs in the length of its body (4.4 SD), less so in the length of its rami (1.7 SD). The mandibular angle is sharper (–2.3 SD), while the gonial angle is markedly larger (3.1 SD). The position of the mandible with respect to the Frankfurt horizontal differs only in the area of the inclination of its rami. Although both jaws differ from the recent group in their protrusion, sagittal intermaxillary relations do not differ significantly.

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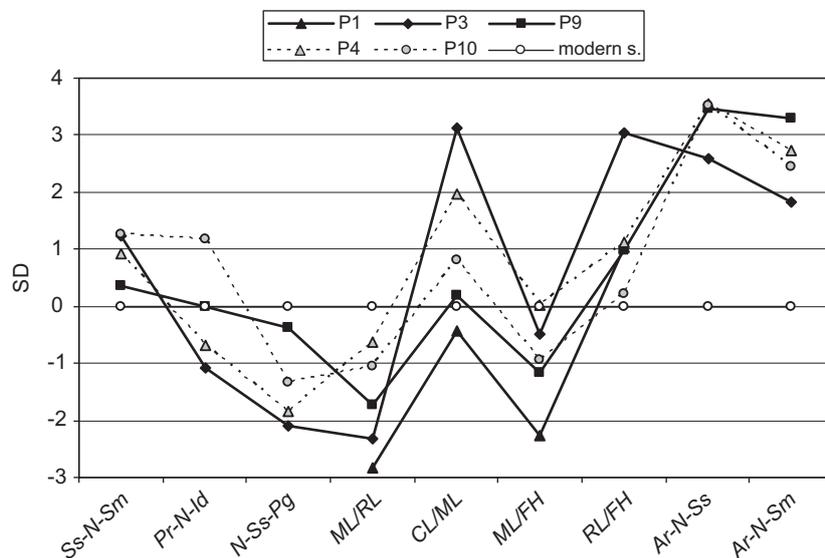


Fig. 9. Plot of the shape differences of the splanchnocranium in the Předmostí fossil skulls sample in relation to the recent reference sample using z -score.

Předmostí skull 9 (P9)

The state of preservation of the male skull P9 enables the evaluation of all the studied variables (Table 1, Figs. 4 and 7–9). Compared to the recent population, the cranium of the skull P9 is longer (3.1 SD) and lower (–1.3 SD). The markedly greater length of the cranium is least of all due to the area of the frontal bone N–B. The angular characteristics of the cranium show no marked differences in shape, compared to the recent population.

The height dimensions of the face correspond to the average of the recent population. The dimensions Ss–Ar (2.7 SD) and Ar–N–Ss (3.5 SD) characterise the greater protrusion of the upper jaw. Similarly, the protrusion of the mandible is characterised by the dimensions Sm–Ar (3.3 SD), Pgn–Ar (2.9 SD) and Ar–N–Sm (3.3 SD). The mandibular body is significantly longer (3.8 SD), but its ramus is longer by only 1 SD. The mandibular angle is sharper (–1.7 SD), but its position with respect to the Frankfurt horizontal does not differ when compared to the recent population. The sagittal inter-maxillary relations are comparable to those of the recent population.

Předmostí skull 4 (P4)

The preservation of the female skull P4 enables the evaluation of all the studied variables (Table 12, Figs. 5 and 7–9). The greatest length of the cranium is 2.1 SD longer than the average of the recent population, while the height of the skull does

not differ. The G–L and L–Ba dimensions are longer in accordance with the greatest length of the cranium. The chords N–B and B–L do not differ significantly. The angular characteristics of the cranium also show no differences in shape, compared to the recent population.

The height dimensions of the face correspond to the average of the recent population. The dimensions Ar–N–Ss (3.5 SD) and N–Ss–Pg (1.8 SD) are in accordance with the greater protrusion of the upper jaw. As to the Ss–Ar dimension, the skull does not differ from the recent population. Both the studied dimensions, Sm–Ar (2.6 SD) and Ar–N–Sm (2.4 SD) correspond to the larger protrusion of the lower jaw. There is the greater convexity of the facial skeleton (–1.8 SD).

The lower jaw of P4 has a markedly longer body (4.5 SD) than the recent population, while the length of the mandibular ramus is shorter by 1.7 SD. The mandibular angle and its position with respect to the Frankfurt horizontal do not differ significantly. The gonial angle is greater by almost 2 SD than the average in the recent population. The sagittal inter-maxillary relations are comparable to the average of the recent (reference) population.

Předmostí skull 10 (P10)

The preservation of the female skull P10 enables the evaluation of all the studied variables, with the exception of the height of the cranium Ba–B and the dimension L–Ba (Table 2, Figs. 5 and 7–9). According to all the variables, the neurocranium does not significantly differ from the reference group. Even the length of the cranium corresponds to the values of the recent population (1.4 SD).

The height dimensions of the face do not differ from those of the recent population. In contrast, the dimensions Ss–Ar (2.7 SD), Ar–N–Ss (3.5 SD) as well as Sm–Ar (2.6 SD) and Ar–N–Sm (2.4 SD) express the marked protrusion of both jaws. The lower jaw of P10 has a significantly longer body (4.5 SD) and the mandibular ramus is actually shorter by 0.75 SD. The mandibular angle is smaller compared to the recent average (–1.1 SD). The gonial angle and the position of the mandible with respect to the Frankfurt horizontal are also identical with those of the recent population. The facial skeleton is slightly more convex (–1.3 SD), the values of the sagittal inter-maxillary relations still correspond to normal occlusion (Ss–N–Sm 4.9°, Pr–N–Id 5.5°).

Metric characteristics of the neurocranium

Differences between the neurocrania of fossil and recent skulls are illustrated in Fig. 7. All fossil skulls are longer (G–Op, G–L), which is more evident in the Předmostí 3 and 9 males, and the height of the skulls is lower (B–Ba; 1.3–1.5 SD). In females, these changes are less pronounced. The modern skulls are shorter on average, but in the only Předmostí female with preserved measurements (P4), B–Ba is less than in the modern Czech sample. The anterior chord of the skull (N–B) is, with the exception of P1 (2.9 SD), not much different from the modern norms (maximal value 1.1 SD), while the posterior chord (B–L) is greater in fossil male

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skulls (1.8–2.9 SD). Skull P1 is characterised by the significantly shortest N–B dimension, which is actually shorter than the average in the recent population.

The overall shape of the neurocranium is also documented by the shape variable (N–B–L), but Figs. 2–6 are more illustrative, showing recent mean craniograms overlaying the fossil skulls of corresponding sex. These figures demonstrate a lower forehead especially in the Předmostí males, and in all specimens a larger brow and a longer, more angular occipital region.

Metric characteristics of the splanchnocranium

The *z*-scores of the linear dimensions are shown in Figs. 8 and 9. The height dimensions of the Upper Palaeolithic splanchnocrania correspond to the values of the recent population. The only exception is the skull P3, whose cranium is more robust overall, and its upper facial height of 79 mm differs from the rest of the fossil skulls by an average of 2 SD.

All the skulls have in common a marked protrusion of the upper and lower jaws, expressed either as the linear (Ss–Ar, Sm–Ar) or angular dimensions (Ar–N–Ss, Ar–N–Sm). This is associated with the most marked sign of the splanchnocrania of Upper Palaeolithic skulls, and that is with the markedly longer body of the lower jaw. The mandibular ramus is only insignificantly longer in the male skulls (around +1 SD). In addition, the female lower jaws in the Gravettian sample have a slightly shorter mandibular ramus (Cd–Go; by about 1 SD) than in the recent population. On average, the mandibular angle (ML/RL) is similar or smaller than that of the recent population; however, the chin angle (CL–ML) is mostly larger. In comparison to the control file, the inclination of the mandibular ramus with respect to the Frankfurt horizontal (RL/FH) is greater and the inclination of the mandibular corpus (ML/FH) is smaller than in the recent population. Other dimensions (Ar–N–Pg) also show the anterior rotation of the fossil skulls compared to the recent population.

Fossil skulls do not differ substantially in their inter-maxillary and inter-alveolar relations (Ss–N–Sm, Pr–N–Id) from those of the recent population. On average, their faces exhibit greater convexity (N–Ss–Pg).

Comparison of Předmostí and Dolní Věstonice

We also compared the two most complete males from Předmostí (P3 and P9) with three male adults from Dolní Věstonice (Table 3), using two linear dimensions (Matiegka, 1934; Sládek et al., 2000) and eight angular variables from Vlček and Šmahel (2002).

The graphic comparison using the *z*-score of selected morphological variables of the male fossil skulls with regard to the recent standard is plotted in Fig. 10. We established the following common morphological features in both Central European samples: longer and narrower neurocranium than that of the recent population, sharper mandibular angle, anterior rotation of the lower jaw, major face convexity, protrusion of the skeletal profile of both jaws (1–5 SD with the exception of DV 14).

Shape similarity between the Upper Palaeolithic and the recent period was evaluated using the aforementioned eight angular dimensions and the method of

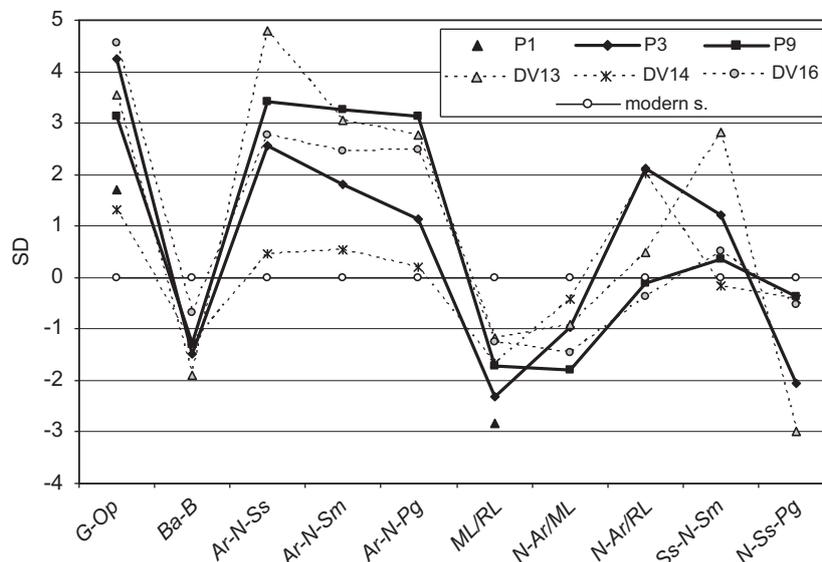


Fig. 10. The comparison of the male fossil skulls from Předmostí and Dolní Věstonice with the recent reference sample using z-score.

cluster analysis. Since the results of cluster tree methods – single linkage, complete linkage, the Ward's method – were very similar, only one dendrogram is shown for males (Fig. 11) and for females (Fig. 12). In both figures, it is evident that the Upper Palaeolithic skulls were clustered to one branch of the dendrogram. Also, these dendrograms illustrate that the Předmostí and Dolní Věstonice profile shapes are distant from the recent Czech skulls. Of the male Palaeolithic skulls, the most similar are skulls P9 and DV16; the least similar skull (in shape) compared to the others is skull P13. This mutual similarity of Palaeolithic skulls can also be seen in Fig. 10. The results of cluster analysis for both sexes confirm that the shape of the skeletal profile of Palaeolithic skulls differs from that of the overall variability in the analysed sample of the recent population.

Discussion and conclusion

Diachronic changes of the skulls of post-Pleistocene populations were studied in various parts of the Old World, such as Southeast Asia (Brown and Maeda, 2004), Sub-Saharan Africa (Henneberg and Steyn, 1993), Europe (Brace et al., 2006). With the exception of the confirmation of craniofacial similarity between the skulls of recent and Minoan populations (Argyropoulos et al., 1989) or the study of the brachycephalization of the populations living in the territory of former Czechoslovakia from the Neolithic Period until modern times (Hanáková and Stloukal, 1990),

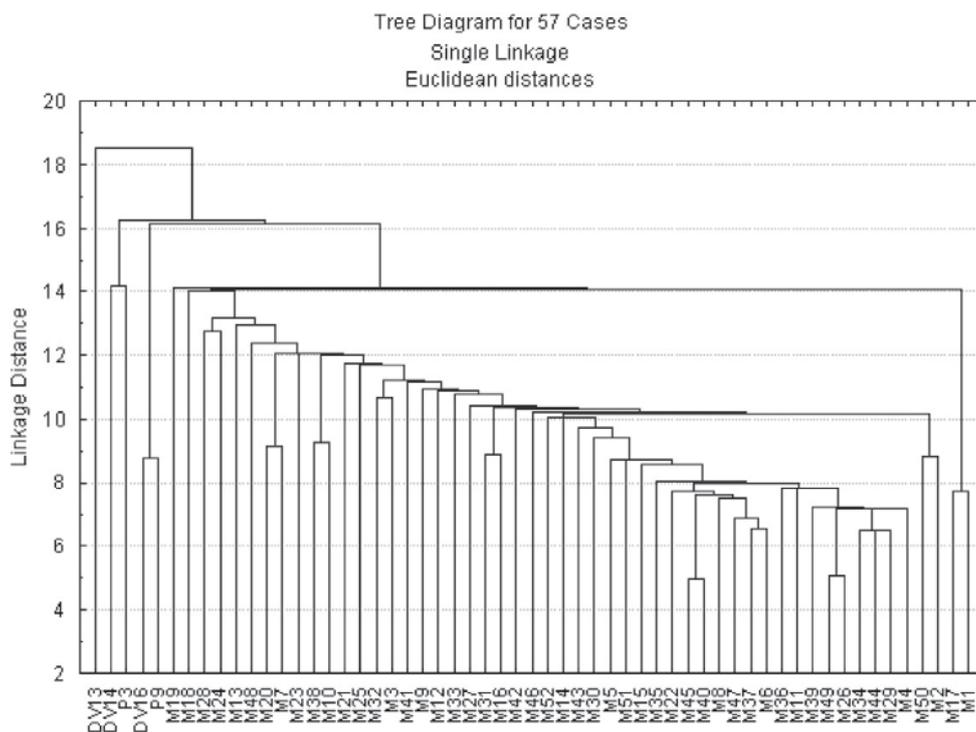


Fig. 11. The cluster analysis (single linkage, Euclidean distances) of recent ($n = 52$) and Upper Palaeolithic ($n = 5$) male skulls samples using the following variables: Ar-N-Ss, Ar-N-Sm, Ar-N-Pg, Ss-N-Sm, N-Ss-Pg, N-Ar/ML, N-Ar/RL, ML/RL.

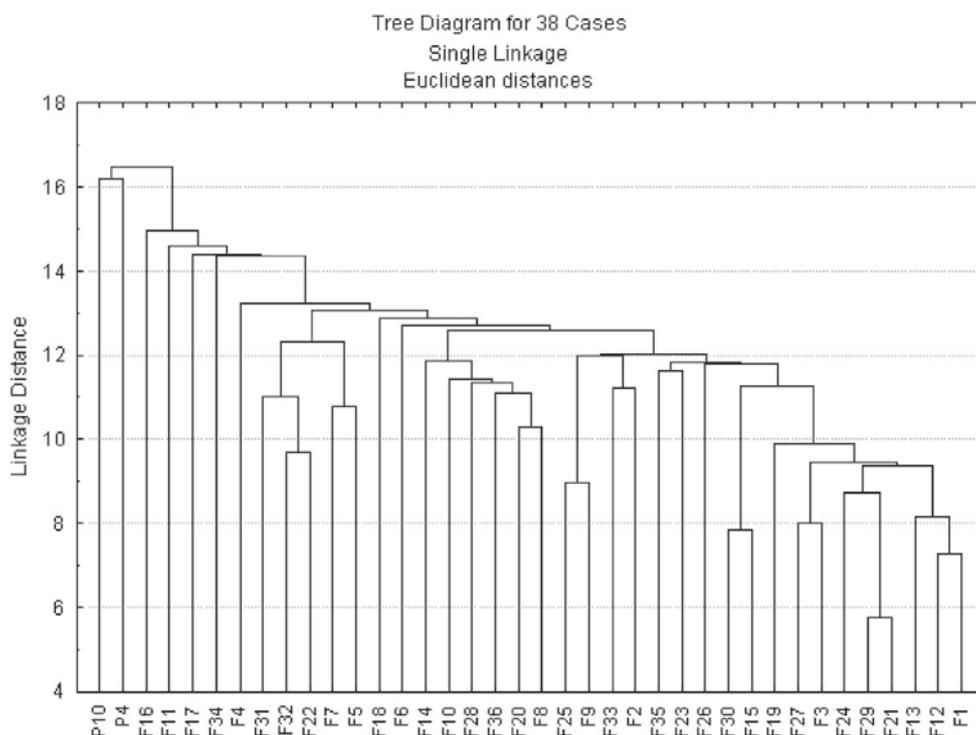


Fig. 12. The cluster analysis (single linkage, Euclidean distances) of recent ($n = 36$) and Upper Palaeolithic ($n = 2$) female skulls samples using the following variables: Ar-N-Ss, Ar-N-Sm, Ar-N-Pg, Ss-N-Sm, N-Ss-Pg, N-Ar/ML, N-Ar/RL, ML/RL.

little attention to date has been paid to the regional analysis of skull changes within small areas such as Central Europe. Study of diachronic trends is related to the issue of population affinity and resemblance. Genetic studies focus on the issue of prehistoric admixture and its traces in the genome of recent human populations (e.g. Semino et al., 2000; Dupanloup et al., 2004; Bauchet et al., 2007). The results of genetic and morphological studies, while both pursue the same goals, cannot be compared directly. The spread of haplo-groups of genetic markers is subordinate to different mechanisms than the genetics of multi-factorial traits such as skeleton dimensions. Evidence for admixture in these dimensions is only rarely studied in humans. It has been documented that major shape differences of the skull are restricted to inter-landmark distances measuring cranial vault length, occipital development, and facial flattening (e.g. Martínez-Abadías et al., 2006). The changes observed in Central European populations in our work support these conclusions. In view of the population movements in the Central European region over the past 30,000 years, we cannot speak about the affinity of the population nor of micro-evolutionary changes, but we retain the neutral term of diachronic change. The mere description of differences of skulls between the Gravettian and recent populations does not explain the observed changes. This is why we are turning both to data of archeogenetics as well as to published data regarding the craniometry of populations from the period between the Upper Palaeolithic and the Modern Age in the area of Czech Republic.

Analysis of hominid cranial morphology is of particular importance for research dealing with questions concerning both the phylogenetic and ontogenetic aspects of the *Homo* genus (Bernhard et al., 2002). The intention of this study was to describe the diachronic changes and variations from the Upper Palaeolithic to the recent period, and to determine to what extent the variation was caused by sexual dimorphism. We confirmed previous findings (Trinkaus and Svoboda, 2006) that Pavlovian samples show heterogeneity in size dimorphism, with homogeneity in overall shape. The same holds true for the Předmostí specimens, with the most robust male skull P3, for which several length (G–Op, B–L) and height dimensions (N–Pr, N–Gn, Id–Gn) differ from other Palaeolithic skulls by at least 1 SD. The supra-orbital projection is similar to that of the Pavlov male and more noticeable than in the Mladeč 5 male. However, distinct lambdoidal flattening is very similar to that in the Mladeč 5 male, as well as in Neandertal males (Frayer et al., 2006).

Despite these differences, if we focus on the dimensions characterising the eight specimens from Předmostí and Dolní Věstonice, the overall differences are not significant. Apart from the typically prolonged neurocranium, they have a markedly longer mandibular body in relation to the mandibular rami, strong protrusion of both jaws, and increased facial convexity with preserved normal sagittal inter-maxillary relations (Ss–N–Sm). The similar shape of the facial skeletal profile is described in many Central EUP fossils (Frayer et al., 2006).

Our comparison of the facial skeletal profile of the Upper Palaeolithic and recent populations revealed size and shape differences of the skulls in the lateral projection. This was caused by markedly longer mandibular bodies. However, female mandibular rami were actually slightly shorter. Both jaws were in strong

protrusion in relation to the cranial base, the face thus developed more towards anterior rotation. Sagittal inter-maxillary relations remained unchanged in relation to recent values. These findings are in agreement with those of Vlček and Šmahel (2002). Besides these shape agreements with the Upper Palaeolithic sample from Dolní Věstonice, a smaller gonial angle and smaller steepness of the mandibular body was evident. The vertical dimensions up to the present have not changed very much. This supports the findings of Manfredi et al. (1997) that the vertical variables are under higher genetic control than the horizontal ones. According to them, heritability seems to have more influence on anterior-vertical dimensions than on posterior dimensions.

The conclusion from these observations is that the recent Central European skulls are significantly shorter in males, even in combination with the higher skull. According to Lieberman et al. (2002), the crania of anatomically modern *H. sapiens* are uniquely characterised by two general structural autapomorphies: facial retraction and neurocranial globularity. Less than 40% of the variation in neurocranial length and height was explained by cranial base breadth and endocranial volume. Similarly shaped features can also be observed in the Sunghir 1 skull from the Upper Palaeolithic period (Alexeeva and Bader, 2000). It is the major difference between the Upper Palaeolithic and recent skulls from the point of view of diachronic trends.

These results are in accordance with the statement (Brace et al., 2006) that craniofacial dimensions, with the exception of the tooth-bearing parts of the facial skeleton, are largely of neutral, adaptive significance. It means that an analysis of their variation can indicate genetic relationships between given populations. The results of the aforementioned study indicate that, in terms of their craniofacial shape, all modern European *H. sapiens* groups show that they are closely related to each other, and that the late Pleistocene skulls are more robust than those of the more recent human groups.

A difference from the present craniofacial shape is considered to be the contribution of the Neolithic population to the variability of the cranial dimensions of the recent European inhabitants (Brace et al., 2006). This is also evidence that the Neolithic people of Europe and their Bronze Age successors are not closely related to the modern inhabitants. It is possible that the variety and extent of the whole European continent does not permit monitoring and observation of diachronic trends that are apparent only in a small region such as the one we have just studied. It also cannot be ruled out that the morphological traits of skulls from the Neolithic until the present have changed significantly.

If we look at cranial length in Bohemia and Moravia (Central Europe) from the Upper Palaeolithic period until today (Neolithic, Eneolithic, Unetice culture, Middle Age) there is clear evidence of brachycephalization, with the lowest average cranial length value found in the recent population. Cranial height in the Neolithic, Eneolithic and the period of Unetice culture is, on average, comparable to that of the recent skulls, while Upper Palaeolithic and early medieval skulls are significantly lower (Černý, 1999; Černý and Velemínský, 1998; Chochol, 1964; Velemínská et al., 2008). Comparison with medieval Czech skulls from the 9th century (Drozdová, 1997;

Velemínská et al., 2008) and another larger sample from the 16–19th century (Hanáková et al., 1984) have indicated a shorter Upper Palaeolithic height of the mandibular ramus and a longer mandibular body.

Current genetic studies show that there is a regional continuity among the inhabitants of the European continent and that the current genetic pool of European populations was affected by both Palaeolithic populations and Neolithic influence from the Near East (Semino et al., 2000; Belle et al., 2006). The estimated proportion of the admixture of European Neolithic populations is 20–50%. The results of the analysis of five individuals, dated between 13,000 and 3000 years BP, have shown the presence of haplotypes common in the current European population (Di Benedeto et al., 2000). Genetic studies of ancient mt-DNA of individuals from the early Neolithic in Central Europe have shown that only 25% of mt-DNA haplotypes of Neolithic farmers originate from the Near East (Haak et al., 2005). This corresponds to the results of recent work on molecular genetics, which shows that around 80% of the genetic make-up of the current population in the Czech territory has its roots in the Upper Palaeolithic (Kráčmarová et al., 2006; Luca et al., 2007). The continuity of settlement of Central Europe from the Upper Palaeolithic period until today was also presumed by Vlček (1991, 1996) on the basis of morphology, especially that of the cranial skeleton.

On the contrary, Van Vark et al. (2003) have argued that morphometric relationships between the crania of EUP inhabitants and modern populations may be a poor indicator for the determination of ancestral–descendant relationships. High variability among EUP crania (Van Vark, 1994) has been consistent with the evidence that only about 10% of modern European mt-DNA had derived from the Early Upper Palaeolithic, while 70% came from Late Upper Palaeolithic, with only 20% originating from the Mesolithic substrate from the Middle East (Sykes, 1999). Nevertheless, according to Jantz and Owsley (2003), Upper Palaeolithic crania are, for the most part, larger and represent more generalised versions of recent European crania. Howells (1995) has reached a similar conclusion with respect to European Mesolithic skulls.

Apparent sexual dimorphism of most size dimensions was detected in recent Central European norms (Šmahel et al., 1998; Macková, 2004) and also in Předmostí and Dolní Věstonice skulls. Franciscus and Vlček (2006) as well, described some level of sexual dimorphism in overall absolute facial height and breadth in the Pavlovian sample. Male crania are more robust with distinctive muscle markings, while females are more slender in many features. According to Wolpoff et al. (2006), Central European Early Upper Palaeolithic male skulls include a constellation of characteristics, beyond just size and muscularity, which represent the retention of Neandertal morphology.

Our results correspond to the micro-evolutionary secular changes described by Wescott and Jantz (2005). This process assumes increasingly stronger expression among the Upper Palaeolithic and recent reference samples, which were the object of our studies. The most typical evolutionary changes were the development of neurocranial globularity and decreased facial convexity. It is hard to define the ultimate causes of the abovementioned craniofacial alterations over time. We are of

the opinion that, in addition to genetic changes and improved health and nutrition (Angel et al., 1987; Jantz and Meadows Jantz, 2000; Kouchi, 2000), biomechanical responses to a more processed diet (Carlson and Van Gerven, 1977; Larsen, 1997) could have had a crucial influence.

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Příloha C

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Limb Bones Asymmetry and Stress in Medieval and Recent Populations of Central Europe

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ABSTRACT Monitoring the degree of asymmetry in different parts of the human body can contribute to population studies, as it may be connected indirectly with the social structure, living conditions, and also with biomechanical stress affecting the person. Analysis of asymmetry may also assess preferential use of the right or left of the body during specific activities. This study is based on the measurements of bones of the upper and lower limbs of skeletons derived from the remarkable medieval cemeteries of Mikulčice-Kostelisko (78 male, 132 female) and Prušánky (66 male, 69 female) (9th–12th centuries AD), and a series of skeletons representing a recent population from Bohemia (143 male, 157 female). The objective was to assess directional asymmetry (DA), fluctuating asymmetry (FA) and antisymmetry (AS) of the dimensions of the evaluated bones, and to use these data to compare the characteristics of the medieval and recent populations. DA was recorded in most dimensions. In the upper limb, the humerus exhibited the greatest expression of asymmetry, and, with the exception of the clavicle, DA was always more pronounced on the right side. Conversely, DA was less prevalent in the lower limb bones. It was more pronounced on the transverse, sagittal and circumferential dimensions of the diaphyses and epiphyses than on the length, and in most cases it was on the left side. The FA values were very low, and almost negligible in relation to the size. Nevertheless, FA was markedly more frequent on the lower than on the upper limb. In contrast to the medieval population, the recent population had higher FA and DA values. Thus, we propose that people from this medieval population were subjected to lower developmental stress than the recent sample. Copyright © 2008 John Wiley & Sons, Ltd.

Key words: medieval population; Great Moravia; recent population; Central Europe; long bones of the upper and lower limb; directional asymmetry; fluctuating asymmetry; stress; developmental stability

Introduction

Asymmetry is a feature commonly found in nature and is one of the fundamental characteristics of living organisms. The human body is also asymmetric – in addition to obvious physical

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asymmetries in the human form, very slight deviations (in the range of 1% or less from a trait size) may develop and these are not immediately observable. These deviations may provide many clues about the person's living conditions, and/or health (Palmer, 1996). But if the deviations are too pronounced, they may be pathological (Burian, 1939). Knowledge of asymmetry may be used for the cognition of the ontogenetic principles, the fitness assessment of organisms, and understanding their developmental stability

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(Palmer, 1996). Through the study of population asymmetry, it is possible, therefore, to compare and contrast different behaviour patterns within and between populations (Ruff & Jones, 1981; Fresia *et al.*, 1990; De Leon, 2007).

Asymmetry may be considered to be the measure of the intensity of specific factors. Besides genetic and hormonal factors (Helmkamp & Falk, 1990) asymmetry may develop as a response to environmental (Schell *et al.*, 1985; Kieser *et al.*, 1986) and biomechanical factors (Graham *et al.*, 1993). Above all, the environmental factors include various stresses, such as malnutrition, excessive noise, cold and heat, which increase asymmetry. The degree of asymmetry may be reflective of biomechanical loading. The location of asymmetrical bone development may be indicative of specific physiological stress. The greater the load affecting the long bones, the stronger the expression of asymmetry (Ruff & Jones, 1981; Schell *et al.*, 1985; Čuk *et al.*, 2001). The age of the individual may be an additional factor (confirmed by Ruff & Jones, 1981; Helmkamp & Falk, 1990; Škvařilová, 1999; not confirmed by Roy *et al.*, 1994; and Plochocki, 2002). The sex of the individual is also taken into account. Here again, the conclusions are contradictory. Schell *et al.* (1985), Roy *et al.* (1994), Steele and Mays (1995) and Škvařilová (1999) did not find sex differences in the degree of asymmetry. In some studies the samples were not divided according to sex (Roy *et al.*, 1994; Čuk *et al.*, 2001). Other studies demonstrate that this factor also contributes to asymmetry (Feik *et al.*, 1996; Lazenby, 2002).

Currently we distinguish several asymmetry types which may manifest in a similar manner but arise from different causes (Palmer, 1994); the three basic types are directional asymmetry, fluctuating asymmetry and antisymmetry. Directional asymmetry (DA) is a type of bilateral asymmetry where in the whole sample a statistically significant difference exists between sides, and the side that is larger is generally the same. The mean of values [right side (R)–left side (L)] differs from zero (Van Valen, 1962; Palmer, 1994). Fluctuating asymmetry (FA) is a type of bilateral asymmetry where the mean value (R–L) is zero and all variations are normally distributed about the mean. It may be assessed only if DA or antisymmetry (AS) is absent (Palmer, 1994). AS is

also the presence of bilateral variation, where a statistically significant difference exists between sides, but the side that is larger varies among individuals. The mean (R–L) is zero and the distribution of variations around this mean is platykurtic or bimodal (Van Valen, 1962).

Investigations were carried out both on skeletal collections (e.g. Stirland, 1993; Albert & Greene, 1999; Plochocki, 2002) and on clinical material (Schell *et al.*, 1985; Roy *et al.*, 1994; Little *et al.*, 2002). The results showed that bilateral asymmetry is commonly expressed more in the upper limb. In conjunction with asymmetry of the upper limb, the term 'handedness' is encountered. This involves a preference for one (right or left) hand for certain actions. Handedness exerts an influence on the asymmetry of the long bones of the limbs: they are longer and larger on the dominant side. The general trend is a preference for the right hand (Steele & Mays, 1995; Čuk *et al.*, 2001); about 90% of people have a more developed right upper limb (the long bones of the right upper limb are 1–3% longer, and 2–4% heavier than the long bones of the left side). The most asymmetric bone is the humerus, by which we can probably assess the preference for the right or left hand, and therefore also the dominance of one or the other upper limb (Čuk *et al.*, 2001). According to Mays *et al.* (1999), the right clavicle is shorter and more robust in most individuals, especially in adults. As a rule, the muscle and ligament insertion sites are larger on the right side.

Commonly (in about 55–75% of people, according to Čuk *et al.*, 2001), the left lower limb is more robust (the results vary with regard to the length; Latimer & Lowrance, 1965; Macho, 1991; Ruff, 1992). The bones of the left lower limb, especially the femur, are longer and heavier on average. The dominant lower limb has a larger tibia, and it is on the opposite side to the dominant upper limb. Disregarding handedness, the left lower limb may be more robust because its function is to support while the right lower limb is used for other functions (e.g. kicking; Singh, 1970; Plato *et al.*, 1985; Macho, 1991; Čuk *et al.*, 2001).

The diaphyseal widths and circumferences are more asymmetric than the maximum lengths of the long bones.

The aim of our research was (a) the verification of DA, FA and AS of the dimensions of the upper

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and lower limb bones in the Central European medieval and recent population; (b) to use these indicators to compare the differences between both populations; (c) to assess the degree of developmental stress affecting the medieval and recent populations.

Material

Two diachronic osteological collections with different expected levels of health/environmental stress were used for the study. Both came from the Central Europe area; the first represents a medieval population from two Slavonic burial grounds dated to the 9th–12th centuries AD, and the second represents a Bohemian population from the first half of the 20th century (the clinical 'Pachner's Collection').

Most evaluated medieval skeletons came from the Great Moravian Empire period and its existence was documented in the first third of the 9th century AD. The Great Moravian Empire is considered to be the first state formation in Central Europe. In the last quarter of the 9th century, in addition to the original South-Moravian centre, the Great Moravian Empire also comprised the territory of Bohemia, southern Poland, western Slovakia and areas adjacent to the Danube and Tisa rivers. It was, therefore, an important political partner to the great medieval European powers such as the Eastern Frankish Kingdom and the Byzantine Empire. Archaeological findings from this and later periods indicate a density of settlements, mostly fortified, in the southern Moravian territory; evidently this area was also an important European trading hub. Mikulčice is considered to have been a major (and perhaps the main) centre. In the early 10th century, Great Moravia was ultimately overrun by Magyar invaders and its remnants were later divided between the kingdoms of Hungary, Bohemia, Poland, and the Holy Roman Empire (e.g. Poláček, 2000). Within the scope of the Mikulčice settlement agglomeration, more than 2500 graves were excavated, mostly from the 9th century. This represents one of the largest, cohesive early medieval population samples in Europe. Mikulčice-Kostelisko is the second most extensive Great Moravian burial ground within the scope of the Mikulčice settlement agglomeration (9th–10th centuries). It is reported to have been the graveyard for inhabitants from the area in front of the castle (e.g. military personnel), but it may also have been a civilian necropolis (for farmers, artisans, and persons of higher social status); 425 graves were found here during excavations (e.g. Poláček & Marek, 2005; Velemínský *et al.*, 2005a).

Prušánky is a necropolis approximately 9 km distant from Mikulčice; 676 graves were excavated pertaining to the 9th and 10th centuries. These contained rural grave goods, and later 10th to 12th century burials contained high status grave goods (e.g. Klanica, 2006).

Only adult individuals whose age range at death and sex could be confidently established were included in this study (e.g. Brůžek, 2002; Dobisíková, 1999). On this basis, 66 male and 69 female skeletons from the Prušánky necropolis and 78 male and 132 female skeletons from the Mikulčice-Kostelisko necropolis were analysed (e.g. Velemínský *et al.*, 2005a). The skeletons are deposited in the Department of Anthropology of the National Museum in Prague.

The 'Pachner's Collection' was used as a recent population comparative. This unique collection consists of more than 300 postcranial skeletons with associated documentation (name, sex, age, height, autopsy year). The collection is from the 1930s and represents Czech inhabitants from lower socio-economic groups (Pachner, 1937). The collection is deposited in the Department of Anthropology and Human Genetics of the Faculty of Science, Charles University in Prague; 143 male and 157 female skeletons were studied.

The long bones of the lower limb (femur, tibia, fibula), and the bones of the upper limb (humerus, radius, ulna, scapula, clavicle) were chosen for analysis. Bones with pathological findings were excluded from this analysis.

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Methods

In asymmetry assessment it is clearly desirable to have dimensions of both left and right bones, and so only cases where the individual's paired bones remained preserved were included.

The defined metric dimensions were measured (Martin & Saller, 1957; Bräuer, 1988) – 21 linear

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dimensions on the upper limb, and 27 linear and circumferential dimensions on the lower limb (for list of dimensions, see Table 1). All adult individuals were assessed together, and both sexes were evaluated separately.

For testing of repeatability, both left and right bones of 16 individuals were remeasured (Steele & Mays, 1995; Mays, 2002). The inter-observer error was calculated using the reliability coefficient of the particular measurements and of asymmetry scores (Fields *et al.*, 1995). The systematic error was assessed using the paired *t*-test. The ANOVA test was used to rule out the FA being caused by measurement error (Roy *et al.*, 1994; Little *et al.*, 2002).

The normal distribution of the difference between the right and the left side was expressed graphically, and so the presence of AS was excluded.

The presence and degree of DA was determined using the paired *t*-test. Dimensions with significant differences ($P \leq 0.05$) between the right and the left sides were considered to be directionally asymmetric. On the remaining dimensions where neither DA nor AS was manifest, the presence of FA was tested using formulae according to Palmer and Strobeck (1986). The values FA1 and FA2 yield information about unsigned (absolute) asymmetry – if, and by how much on average, the magnitudes R and L differ. The values FA4 and FA6 provide information about the direction of the signed asymmetry. FA2 and FA6 are not biased by size dependence of the right–left difference (for the formulae, see Table 5).

The differences between asymmetry in both populations were tested using statistical nonparametric analysis, the Mann Whitney U-test ($P \leq 0.05$). Comparison was made for both sexes separately and also considering all individuals together.

The software STATISTICA version 6.0 (StatSoft, Inc.) and Microsoft Office Excel 2003 were used to carry out the calculations.

Results

No statistically significant differences between repeated measurements were shown in the mea-

surement accuracy test, by reliability coefficient, systematic error testing, or the ANOVA test. But the repeatability of a particular measurement is not an adequate guide to the repeatability of asymmetry scores derived from it, because they depend both on measurement error and on the size of the difference between sides (Fields *et al.*, 1995; Mays, 2002). In particular, in FA assessment the differences between sides are generally small, so the contribution made by measurement errors in asymmetry scores is larger than is the case for raw measurements. Measurement error tends to have a randomising effect on the data. Hence in our study, FA (the greater the measurement error, the greater the impact on the estimate of the subtle asymmetries; Palmer, 1994) was assessed only on dimensions, whereas no measurement error was noted in asymmetry scores.

The graphical analysis showed that the R–L difference was normally distributed and therefore AS did not manifest itself in any trait.

As expected, DA was more frequent for bones of the upper than of the lower limb. In the recent population (Tables 1 and 2), DA was present in all upper limb bones studied in 81% of metric traits in females and 67% in males, and with the exception of the clavicular length it was always in favour of the right side. It was most marked for the humerus (in all dimensions) and the maximum lengths of forearm bones, and least for the dimensions of the scapula. The clavicle was shorter and more robust on the right side in most individuals (Bigoni *et al.*, 2005).

DA in the lower limb of the recent population was recorded only in the dimensions of the femur, and was manifest in 47% of the dimensions in females and 33% of the dimensions in males. DA of the length dimensions and the diaphyseal dimensions was directed to the left, and in epiphyseal dimensions it was directed to the right side. In both sexes, left-side DA was recorded in the physiological length of femur and in most sagittal diaphyseal diameters, and in females moreover in the diaphyseal circumference, and in some transversal diaphyseal diameters. Right-side DA was manifest in the lower epicondylar width in males and the upper width of the epiphysis in females (Bigoni *et al.*, 2005).

In the medieval population (Tables 3 and 4), DA of the upper limb was recorded less frequently

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Table 1. Studied DA: results of paired *t*-tests of males from the recent population

		N	Mean sin	SD	Mean dx	SD	<i>t</i>	<i>P</i>	
SCAPULA									
Anatomical width	Sc1	80	161.9	9.1	161.3	8.6	1.334	0.186	
Anatomical length	Sc2	112	104.6	6.3	104.0	5.8	3.104	0.002**	sin
Length of the margo lateralis	Sc3	112	138.3	8.1	138.0	8.5	1.000	0.319	
CLAVICLE									
Maximum clavicle length	Cl1	97	150.8	8.0	149.2	7.8	3.334	0.001**	sin
Vertical diameter	Cl4	112	11.1	1.3	11.3	1.5	-1.815	0.072	
Sagittal diameter	Cl5	112	12.6	1.4	13.0	1.4	-3.040	0.003**	dx
HUMERUS									
Maximum length of the humerus	H1	117	322.4	17.3	325.7	16.7	-9.933	0.000***	dx
Width of the upper epiphysis	H3	118	50.5	2.3	51.4	2.3	-8.274	0.000***	dx
Width of the lower epiphysis	H4	118	61.7	3.8	62.2	3.9	-3.544	0.001***	dx
Maximum diameter of the middle of the diaphysis	H5	120	23.2	1.9	23.8	2.1	-5.344	0.000***	dx
Minimum diameter of the middle of the diaphysis	H6	120	18.6	1.7	18.9	1.7	-4.698	0.000***	dx
Maximum transverse diameter of the head	H9	112	44.3	2.0	44.7	2.3	-3.145	0.002**	dx
Maximum vertical diameter of the head	H10	118	48.0	2.4	48.5	2.2	-4.148	0.000***	dx
ULNA									
Maximum length of the ulna	U1	100	255.4	13.2	257.5	13.1	-6.387	0.000***	dx
Sagittal diameter of the diaphysis	U11	103	14.3	1.3	14.4	1.4	-0.904	0.368	
Width of the diaphysis	U12	103	17.5	1.4	17.7	1.5	-1.618	0.109	
RADIUS									
Maximum length of the radius	R1	96	237.0	11.9	239.7	12.0	-8.445	0.000***	dx
Maximum width of the diaphysis	R4	97	17.8	1.6	18.2	1.7	-3.523	0.001***	dx
Sagittal diameter of the diaphysis	R5	97	12.4	1.1	12.5	1.1	-1.026	0.308	
Width of the middle of the diaphysis	R4a	98	16.7	1.6	17.3	1.6	-4.570	0.000***	dx
Sagittal diameter of the middle of the diaphysis	R5a	98	12.7	1.1	12.8	1.0	-1.440	0.153	
FEMUR									
Maximum length of the femur	F1	66	451.8	23.5	450.9	22.8	1.457	0.150	
Physiological length	F2	66	449.7	23.2	448.0	22.6	2.761	0.007**	sin
Sagittal diameter of the middle of the diaphysis	F6a	67	28.5	2.4	28.7	2.5	-1.130	0.262	
Transverse diameter of the middle of the diaphysis	F7a	67	28.6	2.4	28.5	2.3	0.639	0.525	
Upper transverse diameter of the diaphysis	F7b	67	30.8	2.7	30.6	2.7	1.390	0.169	
Upper sagittal diameter of the diaphysis	F7c	67	28.7	2.2	28.0	2.3	5.457	0.000***	sin
Lower transverse diameter of the diaphysis	F7d	67	35.9	4.0	35.7	4.1	0.878	0.383	
Lower sagittal diameter of the diaphysis	F7e	67	31.7	3.1	31.1	2.9	4.243	0.000***	sin
Subtrochanteric transverse diameter of the diaph.	F9	67	33.7	2.6	33.7	2.6	-0.168	0.867	
Subtrochanteric sagittal diameter of the diaphysis	F10	67	28.9	2.2	28.5	2.2	2.690	0.009**	sin
Circumference of the middle of the diaphysis	F8	67	87.3	5.7	87.2	5.7	0.521	0.604	
Upper width of the epiphysis	F13	66	101.8	6.3	102.0	5.9	-0.327	0.745	
Epicondylar width	F21	67	82.1	4.5	82.8	4.5	-3.339	0.001**	dx
Vertical diameter of the head	F18	66	48.6	2.6	48.8	2.7	-0.976	0.333	
Transverse diameter of the head	F19	66	48.3	2.4	48.4	2.7	-0.757	0.452	
FIBULA									
Maximum length of the fibula	Fi1	93	359.2	24.6	359.3	23.8	-0.170	0.865	

(Continues)

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Table 1. (Continued)

		N	Mean sin	SD	Mean dx	SD	<i>t</i>	<i>P</i>
TIBIA								
Overall length tibiae	T1	47	367.2	21.4	367.7	20.8	-0.622	0.537
Medial length	T1b	46	356.8	20.3	357.5	20.5	-0.811	0.422
Maximum width of the upper epiphysis	T3	46	74.6	2.9	74.2	3.0	2.008	0.051
Width of the lower epiphysis	T6	47	48.5	3.0	48.1	2.9	1.449	0.154
Minimum diameter of the middle of the diaphysis	T8	53	29.4	2.7	29.5	2.3	-0.855	0.396
Width of the middle of the diaphysis	T9	53	22.7	2.0	22.6	2.1	0.484	0.630
Sagittal diameter in the upper foramen nutricium	T8a	51	33.8	3.3	33.7	3.0	0.409	0.684
Width of the diaphysis in the upper for. nutric.	T9a	51	25.0	2.1	25.1	2.4	-0.461	0.647
Circumference of the middle of the diaphysis	T10	53	80.4	5.9	79.8	5.6	1.965	0.055
Circumference of the diaphysis on the for. nutric.	T10a	51	91.2	7.3	91.0	6.8	0.446	0.657
Minimum circumference of the diaphysis	T10b	53	71.8	5.1	71.7	4.9	0.778	0.440

Averages are specified in mm.

N, number of dimensions (df = N-1); SD, standard deviation; *P* significance levels:

* = 5%.

** = 1%.

*** = 0.1%.

than in the recent population (in 38% of metric traits in females and 48% in males). It was most pronounced in the lengths of all the long bones, except for the clavicle. With regard to sexual dimorphism there were some differences. On the humerus and radius, DA was manifest in males almost in all dimensions, in females only in the maximum lengths and also on certain diaphyseal diameters of these bones. Conversely, the ulna was more asymmetric in females (DA seen in all dimensions).

For the lower limb dimensions of the medieval population, DA was recorded more frequently than in the recent population and it was always directed to the left. It was manifest for the femur in 53% of traits in males, 33% in females; for the tibia of both sexes in 18% of traits. For the femur in males, DA was recorded in the length dimensions, in most diaphyseal diameters, and also in the diaphyseal circumference. In females it was less frequent; it was observed in the physiological length, in certain transversal diameters, and in the lower sagittal diaphyseal diameter. The most significant deviations were in the transversal diaphyseal diameter. For the tibia, DA was manifest in both sexes in the overall length, in males in the diaphyseal circumference, and in females in the medial length.

As for the statistical tests evaluating DA differences between populations, some findings were recorded (see Table 7). Using the Mann-Whitney U-test, approximately 22.2% of all linear distances (10 out of a total of 45 traits) showed significantly different levels of DA between the medieval and recent populations. Of these, 70% (7/10) were more asymmetric in the recent group. Of interest is the result when considering sexes separately. In males, both groups differed in 15.6% (7/45) of samples, while in females it was only 4.4% (2/45).

In both populations, FA (Tables 5 and 6) of the bones of the upper limb was minimal; on the lower limb it was more frequent, but even here its values were very low. FA attained the highest values in the length dimensions (FA1, FA4), but if FA values were related to the size of the measured trait it was almost negligible (FA2, FA6). FA of the recent population reached higher values in both upper and lower limbs than in the medieval population. In the upper limb of the recent population, the highest FA was in the scapula dimensions; the medieval population had higher FA values in the clavicle and the maximal length of the ulna. In both populations, lower limb FA reached the highest values in lengths and in circumferential dimensions in the tibia and on the upper epiphysis of the femur.

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Table 2. Studied DA: results of paired *t*-tests of females from the recent population (for legend, see Table 1)

		N	Mean sin	SD sin	Mean dx	SD dx	<i>t</i>	<i>P</i>	
SCAPULA									
Anatomical width	Sc1	78	144.3	9.0	144.4	8.9	-0.076	0.939	
Anatomical length	Sc2	112	96.6	5.5	96.7	5.6	-0.343	0.733	
Length of the margo lateralis	Sc3	106	125.2	8.9	126.3	8.8	-4.003	0.000***	dx
CLAVICLE									
Maximum clavicle length	Cl1	75	136.1	7.1	134.4	7.1	4.548	0.000***	sin
Vertical diameter	Cl4	108	9.1	1.3	9.2	1.2	-0.465	0.643	
Sagittal diameter	Cl5	108	10.9	1.2	11.4	1.3	-4.696	0.000***	dx
HUMERUS									
Maximum length of the humerus	H1	125	297.7	15.2	301.2	15.2	-10.003	0.000***	dx
Width of the upper epiphysis	H3	125	44.8	2.5	45.5	2.6	-7.016	0.000***	dx
Width of the lower epiphysis	H4	126	54.0	3.2	54.8	3.3	-5.608	0.000***	dx
Maximum diameter of the middle of the diaph.	H5	127	20.6	1.6	21.2	1.6	-6.655	0.000***	dx
Minimum diameter of the middle of the diaph.	H6	127	16.2	1.4	16.4	1.5	-3.675	0.000***	dx
Maximum transverse diameter of the head	H9	112	39.0	2.0	39.5	2.2	-4.578	0.000***	dx
Maximum vertical diameter of the head	H10	119	42.1	2.2	42.5	2.5	-3.214	0.002**	dx
ULNA									
Maximum length of the ulna	U1	118	230.8	11.6	234.0	12.2	-10.806	0.000***	dx
Sagittal diameter of the diaphysis	U11	126	11.9	1.1	12.2	1.1	-4.024	0.000***	dx
Width of the diaphysis	U12	126	15.0	1.2	15.3	1.3	-4.887	0.000***	dx
RADIUS									
Maximum length of the radius	R1	123	212.8	11.7	216.3	12.2	-9.617	0.000***	dx
Maximum width of the diaphysis	R4	128	15.6	1.6	15.9	1.5	-4.078	0.000***	dx
Sagittal diameter of the diaphysis	R5	128	10.6	0.8	10.6	0.8	-0.961	0.338	
Width of the middle of the diaphysis	R4a	128	14.7	1.4	15.1	1.4	-6.121	0.000***	dx
Sagittal diameter of the middle of the diaphysis	R5a	128	10.6	0.8	10.7	0.8	-2.350	0.020*	dx
FEMUR									
Maximum length of the femur	F1	58	415.0	19.2	414.6	19.6	0.681	0.499	
Physiological length	F2	58	411.6	19.3	410.5	19.8	2.106	0.040*	sin
Sagittal diameter of the middle of the diaphysis	F6a	64	25.9	2.0	25.9	2.2	-0.244	0.808	
Transverse diameter of the middle of the diaphysis	F7a	64	26.8	2.5	26.5	2.2	2.116	0.038*	sin
Upper transverse diameter of the diaphysis	F7b	64	29.3	2.6	28.6	2.8	3.550	0.001***	sin
Upper sagittal diameter of the diaphysis	F7c	64	25.7	2.3	25.2	2.1	2.657	0.010**	sin
Lower transverse diameter of the diaphysis	F7d	64	33.0	3.7	33.0	3.8	0.000	1.000	
Lower sagittal diameter of the diaphysis	F7e	64	28.7	2.2	28.0	2.4	3.832	0.000***	sin
Subtrochanteric transverse diameter of the diaph.	F9	63	31.5	2.3	31.2	2.5	1.474	0.146	
Subtrochanteric sagittal diameter of the diaphysis	F10	63	25.9	1.9	25.9	2.2	0.000	1.000	
Circumference of the middle of the diaphysis	F8	65	80.2	5.9	79.6	5.6	2.100	0.040*	sin
Upper width of the epiphysis	F13	59	88.1	5.6	88.6	5.8	-2.151	0.036*	dx
Epicondylar width	F21	59	73.8	3.9	73.9	3.8	-0.769	0.445	
Vertical diameter of the head	F18	58	43.1	2.8	43.1	2.9	-0.136	0.892	
Transverse diameter of the head	F19	58	42.5	2.2	42.7	2.3	-1.763	0.083	
FIBULA									
Maximum length of the fibula	Fi1	81	328.6	16.4	328.3	16.6	0.762	0.449	

(Continues)

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Table 2. (Continued)

		N	Mean sin	SD sin	Mean dx	SD dx	<i>t</i>	<i>P</i>
TIBIA								
Overall length tibiae	T1	63	338.5	17.5	337.9	17.2	1.257	0.214
Medial length	T1b	59	329.4	17.6	328.9	17.4	1.137	0.260
Maximum width of the upper epiphysis	T3	55	66.7	3.4	66.6	3.7	0.457	0.649
Width of the lower epiphysis	T6	54	44.0	2.6	44.1	2.7	-0.339	0.736
Minimum diameter of the middle of the diaphysis	T8	69	26.6	2.4	26.7	2.5	-0.173	0.863
Width of the middle of the diaphysis	T9	69	20.6	1.9	20.8	2.3	-1.396	0.167
Sagittal diameter in the upper foramen nutricium	T8a	69	29.9	2.6	29.9	2.5	0.346	0.730
Width of the diaphysis in the upper for. nutric.	T9a	69	22.2	2.0	22.3	2.3	-0.956	0.343
Circumference of the middle of the diaphysis	T10	70	72.1	4.9	72.1	6.0	-0.082	0.935
Circumference of the diaphysis on the for. nutric.	T10a	70	80.8	5.4	80.9	6.1	-0.271	0.788
Minimum circumference of the diaphysis	T10b	71	65.5	4.4	65.6	4.8	-0.518	0.606

Statistical analysis used to compare FA in both populations showed that the medieval population had more traits with significantly lower levels of FA (see Table 7). Specifically, 9.1% of traits (4/45) were of a statistically different level of FA, and 75% (3/4) of these were less asymmetric in the medieval population. In addition, when considering $P \leq 0.06$, then 17.8% of all linear distances (8/45) showed significantly different levels of FA between both populations, and 87.5% (7/8) of these were more asymmetric in the recent population. As well as in DA, there are considerable differences when analysing both sexes separately. Whereas in males, values of FA differed significantly in 8.9% (4/45) of traits and all were more asymmetric in the recent population, in females it was 4.4% (2/45) with greater asymmetry in the medieval population.

Discussion

If asymmetry is considered indicative of non-specific stress affecting the human, it could also be indirectly connected with the social structure of society, the quality of living conditions (nutrition, individual health, degree of stress of different origins; e.g. Graham *et al.*, 1993; Livshits *et al.*, 1998), and also with influences from biomechanical stress (Roy *et al.*, 1994), or with the activities

carried out together with a preference for the right or left side of the body (Steele & Mays, 1995).

In most of the upper limb bones, DA was exhibited for their maximum lengths, and irregularly for the diaphyseal diameters. Whereas in the medieval population it appeared in 43% of traits, in the recent population it was 74%. As the recent population was of a lower social status, non-specific stress may have been a causative factor due to a challenging environment, for example, insufficient nutrition and protracted exposure to unhealthy living conditions (e.g. Graham *et al.*, 1993; Livshits *et al.*, 1998). Again, Steele and Mays (1995) presumed that the DA of limb bones develops as a consequence of greater mechanical stress affecting the dominant limb, and that it increases with age (prolonged stress). It is possible that in individuals from the recent population the dominant upper limb was submitted to greater stress.

Compared with earlier investigations (Steele & Mays, 1995; Mays *et al.*, 1999; Čuk *et al.*, 2001) on handedness, the results of this study demonstrated 81% right-hand dominance. Therefore, the majority of individuals with right-hand dominance had a shorter and more robust right clavicle, and primarily longer and slightly more robust long bones of their right upper limbs. The differences were mostly expressed on the humerus.

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Table 3. Studied DA: results of paired *t*-tests of males from the medieval population (for legend, see Table 1)

Measure		N	Mean sin	SD sin	Mean dx	SD dx	<i>t</i>	<i>P</i>	
CLAVICLE									
Maximum clavicle length	Cl1	8	151.8	13.0	149.9	13.7	0.535	0.609	
Vertical diameter	Cl4	39	11.1	1.4	11.5	1.5	-1.833	0.075	
Sagittal diameter	Cl5	39	12.7	1.2	12.9	1.5	-1.062	0.295	
HUMERUS									
Maximum length of the humerus	H1	24	328.3	17.2	333.6	16.1	-6.226	0.000***	dx
Width of the upper epiphysis	H3	11	49.4	2.6	50.5	2.8	-3.357	0.007**	dx
Width of the lower epiphysis	H4	20	62.8	4.2	63.9	3.7	-3.399	0.003**	dx
Maximum diameter of the middle of the diaphysis	H5	58	22.8	1.7	23.8	1.9	-7.856	0.000***	dx
Minimum diameter of the middle of the diaphysis	H6	60	18.5	1.5	18.9	1.6	-2.572	0.013*	dx
Maximum transverse diameter of the head	H9	3	42.3	2.5	44.0	2.6	-2.500	0.130	
Maximum vertical diameter of the head	H10	10	45.9	7.4	47.1	8.1	-3.343	0.009**	dx
ULNA									
Maximum length of the ulna	U1	12	273.8	14.4	275.1	14.3	-1.470	0.170	
Sagittal diameter of the diaphysis	U11	37	14.4	1.7	14.9	1.5	-3.074	0.004**	dx
Width of the diaphysis	U12	36	17.7	2.0	17.6	1.7	0.373	0.711	
RADIUS									
Maximum length of the radius	R1	13	245.0	20.2	246.2	19.7	-2.259	0.043*	dx
Maximum width of the diaphysis	R4	26	17.5	1.5	18.2	1.2	-3.241	0.003**	dx
Sagittal diameter of the diaphysis	R5	27	12.3	1.2	12.5	1.2	-1.412	0.170	
Width of the middle of the diaphysis	R4a	27	16.5	1.6	16.9	1.5	-2.294	0.030*	dx
Sagittal diameter of the middle of the diaphysis	R5a	26	12.2	0.8	12.4	0.8	-1.413	0.170	
FEMUR									
Maximum length of the femur	F1	28	451.5	26.8	449.7	27.3	2.120	0.043*	
Physiological length	F2	42	450.8	26.1	449.4	26.3	2.117	0.040*	
Sagittal diameter of the middle of the diaphysis	F6a	67	28.8	2.6	28.7	2.8	0.394	0.695	
Transverse diameter of the middle of the diaphysis	F7a	65	29.0	2.5	28.1	2.3	7.913	0.000***	
Upper transverse diameter of the diaphysis	F7b	60	32.3	2.4	31.0	3.0	4.347	0.000***	
Upper sagittal diameter of the diaphysis	F7c	62	27.4	2.5	27.1	2.8	2.537	0.014*	
Lower transverse diameter of the diaphysis	F7d	53	35.5	4.1	34.9	3.9	3.951	0.000***	sin
Lower sagittal diameter of the diaphysis	F7e	53	31.0	2.6	30.9	2.5	0.513	0.610	
Subtrochanteric transverse diameter of the diaph.	F9	69	34.7	2.6	33.8	2.5	4.626	0.000***	sin
Subtrochanteric sagittal diameter of the diaphysis	F10	69	27.9	2.5	27.7	2.1	1.656	0.102	
Circumference of the middle of the diaphysis	F8	55	89.7	5.8	89.0	5.7	2.390	0.020*	sin
Upper width of the epiphysis	F13	35	100.5	7.8	100.6	7.7	-0.193	0.848	
Epicondylar width	F21	14	81.9	5.3	81.9	5.2	-0.234	0.818	
Vertical diameter of the head	F18	33	48.6	2.3	48.6	2.4	0.000	1.000	
Transverse diameter of the head	F19	24	48.0	2.3	48.4	2.9	-1.895	0.071	
TIBIA									
Overall length tibia	T1	25	378.3	25.2	376.4	24.8	3.201	0.004**	sin
Medial length	T1b	17	375.2	26.3	373.6	26.0	1.765	0.097	
Maximum width of the upper epiphysis	T3	4	77.0	0.8	74.8	1.5	2.029	0.135	
Width of the lower epiphysis	T6	12	47.9	4.2	47.8	4.2	0.432	0.674	
Minimum diameter of the middle of the diaphysis	T8	49	29.1	2.6	29.3	2.3	-1.070	0.290	
Width of the middle of the diaphysis	T9	50	22.2	2.1	22.2	2.0	-0.330	0.743	
Sagittal diameter in the upper foramen nutricium	T8a	58	33.3	3.3	33.3	2.9	-0.275	0.784	
Width of the diaphysis in the upper for. nutric.	T9a	59	23.9	2.4	23.9	2.2	-0.219	0.827	

(Continues)

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Table 3. (Continued)

Measure		N	Mean sin	SD sin	Mean dx	SD dx	<i>t</i>	<i>P</i>	
Circumference of the middle of the diaphysis	T10	47	79.9	5.3	79.6	5.2	0.975	0.335	
Circumference of the diaphysis on the for. nutric.	T10a	56	90.3	6.6	89.5	6.2	2.064	0.044*	sin
Minimum circumference of the diaphysis	T10b	54	72.8	5.6	72.5	4.5	0.664	0.510	

In accordance with most studies (*inter alia*: Škvařilová, 1999; Čuk *et al.*, 2001) DA in lower limbs appeared much less than in the upper limb, and this applied to both populations. In the majority of cases (27 out of a total of 29 traits), it was directed to the left, and thus confirmed the greater robustness of the left lower limb due to the effects of stress during life (Čuk *et al.*, 2001). The studied sample of recent skeletons showed DA only in the femur; in the medieval sample it also appeared in certain dimensions of the tibia.

In previous studies, DA was not often found in the bone lengths but only in their robustness (Latimer & Lowrance, 1965; Singh, 1970; Ruff, 1992). To a certain extent, this is in accord with our results; we found more pronounced DA in the dimensions measured on the diaphyses of the bones than for their lengths. According to Čuk *et al.* (2001), this might be due to the fact that longitudinal bone growth is completed between the 18th and 25th year of age, but width growth of the bones continues throughout life.

The left femur had a more robust diaphysis in both populations (similar to prior studies: Ruff & Hayes, 1983; Macho, 1991; Velemínský, 2000; Čuk *et al.*, 2001). According to the authors, it was mainly due to stress resulting from the supporting function of the left lower limb. It was interesting, however, that the femur of the recent sample of females exhibited DA slightly more often than for the medieval females (47% of traits in recent females, compared with 33% of traits in medieval females). The lower limb of medieval males exhibited DA more often than in recent males (38% of traits in medieval males compared with 19% of traits in recent males). In addition, recent males – in contrast to the medieval males – had less sagittal flattening in their left femoral diaphyses than their right. In contrast, medieval males had a

wider left femur in the transversal direction. In the recent population the epiphyseal femoral dimensions showed DA in favour of the right side. According to Čuk *et al.* (2001) this might be the result of stress affecting the knee (and the hip) of the right lower limb which does not have a supporting function.

The more robust diaphysis of the left tibia in males from the Middle Ages could be connected with the dominance expression of the left lower limb (on the opposite side to that of the dominant upper limb; Čuk *et al.*, 2001).

In the recent population, DA occurred more often in females, in accordance with the study of Schultz (1937) (in 41% of traits in males, 52.3% in females). Conversely, in the medieval population DA occurred more often in males (45% in males, 34% in females), as was confirmed by the investigations of Schell *et al.* (1985) or Lazenby (2002), who suggested that females are better able to buffer the detrimental effects of environmental stress. In recent females, DA occurred in most dimensions of the upper limb (in 81% of monitored traits), while for recent males it was present in 67%. In the medieval population DA was manifest in 48% of traits in males (mostly on the humerus); in females it occurred in 38% of traits (mostly on the ulna). Velemínský (2000) similarly confirmed greater asymmetry of the femur in males from the Mikulčice-Kostelisko necropolis, while Ruff and Hayes (1983) found more asymmetric femora in females. In accord with this study, Ruff (1992) did not register sexual differences in femur length asymmetry. Based on these observations, it was not possible to establish unequivocally whether males or females were in general 'more asymmetric'.

The method used by Palmer and Strobeck (1986) was chosen to assess FA. The evaluation of

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Table 4. Studied DA: results of paired *t*-tests of females from the medieval population (for legend, see Table 1)

		N	Mean sin	SD sin	Mean dx	SD dx	<i>t</i>	<i>P</i>	
CLAVICLE									
Maximum clavicle length	C11	17	132.2	8.9	131.0	8.6	1.605	0.128	
Vertical diameter	C14	39	9.6	0.9	9.6	1.1	0.198	0.844	
Sagittal diameter	C15	40	10.6	1.2	10.7	1.1	-0.781	0.440	
HUMERUS									
Maximum length of the humerus	H1	30	290.6	15.8	293.6	15.1	-4.280	0.000 ***	dx
Width of the upper epiphysis	H3	23	43.6	2.5	44.2	2.8	-1.845	0.079	
Width of the lower epiphysis	H4	23	54.5	2.8	55.2	3.0	-2.626	0.015 *	dx
Maximum diameter of the middle of the diaph.	H5	64	20.1	1.5	20.5	1.5	-3.291	0.002 **	dx
Minimum diameter of the middle of the diaph.	H6	66	15.5	1.3	15.8	1.4	-1.626	0.109	
Maximum transverse diameter of the head	H9	10	38.6	2.0	39.4	1.3	-2.228	0.053	
Maximum vertical diameter of the head	H10	20	41.5	2.4	41.3	2.4	1.045	0.309	
ULNA									
Maximum length of the ulna	U1	15	239.8	7.7	242.3	8.4	-3.510	0.003 **	dx
Sagittal diameter of the diaphysis	U11	42	11.6	1.3	12.1	1.5	-3.490	0.001 **	dx
Width of the diaphysis	U12	42	14.5	1.6	14.9	1.6	-2.638	0.012 *	dx
RADIUS									
Maximum length of the radius	R1	17	214.6	13.6	217.8	13.9	-6.246	0.000 ***	dx
Maximum width of the diaphysis	R4	33	15.1	1.2	15.4	1.4	-2.101	0.044	
Sagittal diameter of the diaphysis	R5	36	10.6	1.1	10.9	1.2	-2.142	0.039 *	dx
Width of the middle of the diaphysis	R4a	35	14.0	1.3	14.3	1.6	-1.819	0.078	
Sagittal diameter of the middle of the diaphysis	R5a	33	10.5	0.8	10.4	0.9	0.571	0.572	
FEMUR									
Maximum length of the femur	F1	47	410.3	17.6	409.4	18.0	1.872	0.068	
Physiological length	F2	57	406.4	14.5	405.0	14.7	2.909	0.005 **	sin
Sagittal diameter of the middle of the diaphysis	F6a	96	24.5	2.4	24.3	2.3	1.520	0.132	
Transverse diameter of the middle of the diaphysis	F7a	95	25.7	2.0	25.3	2.0	3.956	0.000 ***	sin
Upper transverse diameter of the diaphysis	F7b	78	29.2	2.4	28.9	2.6	1.828	0.071	
Upper sagittal diameter of the diaphysis	F7c	76	23.4	2.4	23.3	2.6	0.681	0.498	
Lower transverse diameter of the diaphysis	F7d	74	31.4	3.6	30.9	3.4	3.158	0.002 **	sin
Lower sagittal diameter of the diaphysis	F7e	73	26.5	2.5	26.2	2.3	2.021	0.047 *	sin
Subtrochanteric transverse diameter of the diaph.	F9	89	31.0	2.4	30.9	2.5	0.600	0.550	
Subtrochanteric sagittal diameter of the diaphysis	F10	89	23.9	2.3	23.9	2.5	-0.478	0.634	
Circumference of the middle of the diaphysis	F8	70	79.1	5.4	78.7	5.4	2.159	0.034 *	sin
Upper width of the epiphysis	F13	45	88.5	5.4	88.6	6.1	-0.380	0.705	
Epicondylar width	F21	21	71.9	2.8	72.0	3.4	-0.149	0.883	
Vertical diameter of the head	F18	40	42.4	2.2	42.5	2.2	-0.552	0.584	
Transverse diameter of the head	F19	34	41.7	2.1	41.9	2.1	-1.643	0.110	
TIBIA									
Overall length tibia	T1	31	336.7	15.1	335.4	15.5	2.599	0.014 *	sin
Medial length	T1b	23	329.7	15.7	328.0	15.7	3.169	0.004 **	sin
Maximum width of the upper epiphysis	T3	7	65.6	1.7	66.1	2.4	-0.934	0.386	
Width of the lower epiphysis	T6	18	42.0	2.5	41.9	2.3	0.270	0.790	
Minimum diameter of the middle of the diaphysis	T8	56	26.6	2.1	26.6	2.1	0.000	1.000	
Width of the middle of the diaphysis	T9	57	19.9	2.1	20.1	2.0	-0.714	0.478	
Sagittal diameter in the upper foramen nutricium	T8a	66	30.2	2.3	30.0	2.4	0.745	0.459	
Width of the diaphysis in the upper for. nutric.	T9a	69	21.3	2.2	21.4	1.9	-0.860	0.393	
Circumference of the middle of the diaphysis	T10	56	71.6	4.7	71.9	5.0	-1.166	0.249	
Circumference of the diaphysis on the for. nutric.	T10a	70	80.2	5.6	80.2	6.2	-0.276	0.784	
Minimum circumference of the diaphysis	T10b	63	66.1	3.9	66.1	3.7	-0.278	0.782	

FA is problematic, since the effects of AS or DA must be filtered from the analysis. When studying FA, it is very important to remove or qualify the measurement error. In this study the measurement of the bones of 16 individuals was repeated (Steele & Mays, 1995; Mays *et al.*, 1999). FA was assessed

only in dimensions where no measurement error of raw measurement or asymmetry scores was recorded (Fields *et al.*, 1995; Mays, 2002). In our study FA values were very low, and if related to the size of the measured trait it was negligible. In spite of the low values, in the recent population

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Table 5. Results of evaluation of the FA from the recent population

	FA1	FA2	FA4	FA6
<i>Males</i>				
Sc1	2.925	0.018	13.423	0.001
Sc3	2.304	0.017	8.917	0.000
Cl4	0.821	0.073	1.301	0.010
U12	0.602	0.034	0.719	0.002
F1	3.500	0.008	22.845	0.000
F6a	0.985	0.034	2.255	0.003
F7a	0.970	0.034	1.765	0.002
F8	1.567	0.018	4.385	0.001
F13	2.364	0.023	8.955	0.001
F19	0.864	0.018	1.277	0.001
Fi1	2.559	0.007	13.243	0.000
T1	3.574	0.010	30.973	0.000
T1b	3.957	0.011	37.410	0.000
T3	1.217	0.016	2.554	0.000
T6	1.167	0.024	2.608	0.001
T8	1.132	0.040	2.530	0.003
T9	1.000	0.044	1.972	0.004
T8a	1.235	0.037	2.873	0.003
T9a	0.863	0.034	1.445	0.002
T10	1.358	0.017	3.759	0.001
T10a	2.157	0.024	9.648	0.001
T10b	1.170	0.016	3.059	0.001
<i>Females</i>				
Sc1	2.981	0.015	19.230	0.001
Sc2	1.723	0.018	6.110	0.001
Cl4	0.713	0.078	1.063	0.013
F1	3.517	0.008	21.070	0.000
F6a	0.813	0.031	1.030	0.002
F19	0.397	0.009	0.441	0.000
Fi1	2.296	0.007	8.408	0.000
T1	2.794	0.008	12.816	0.000
T1b	2.966	0.009	13.420	0.000
T3	1.364	0.020	4.184	0.001
T6	0.796	0.018	1.423	0.001
T8	0.928	0.035	1.912	0.003
T9	0.765	0.035	1.458	0.003
T8a	0.957	0.032	1.910	0.002
T9a	0.629	0.028	1.001	0.002
T10	1.543	0.020	8.342	0.001
T10a	1.300	0.016	4.809	0.001
T10b	1.099	0.016	3.311	0.001

FA1, FA2, FA4, FA6: indices of the calculation of FA values.

FA1: $\text{mean}\{(R-L)/[(R+L)/2]\}$; FA2: $\text{mean}\{(R-L)/[(R+L)/2]\}$; FA4: $\text{var}\{(R-L)/[(R+L)/2]\}$; FA6: $\text{var}\{(R-L)/[(R+L)/2]\}$.

higher values of FA were noted, particularly in the scapula. In the medieval population, relatively higher FA values appeared in the clavicle. A possible explanation is that DA appears often in this dimension (Mays *et al.*, 1999), but this was not confirmed in our sample.

With regard to the lower limb, the highest variance values (FA4) and absolute FA deviations

Table 6. Results of evaluation of the FA from the medieval population (for legend, see Table 5)

	FA1	FA2	FA4	FA6
<i>Males</i>				
Cl1	6.875	0.046	85.859	0.004
Cl4	0.949	0.084	1.673	0.012
U1	2.500	0.009	9.056	0.000
F6a	0.866	0.030	1.519	0.002
F13	1.200	0.012	2.968	0.000
F19	0.458	0.012	0.901	0.000
T1b	2.941	0.008	12.014	0.000
T6	0.417	0.009	0.410	0.000
T8	0.878	0.031	1.415	0.002
T9	0.560	0.025	0.718	0.001
T8a	1.483	0.045	3.581	0.003
T9a	0.847	0.035	1.389	0.002
T10	1.617	0.020	4.294	0.001
T10b	1.259	0.018	2.497	0.000
<i>Females</i>				
Cl1	2.529	0.019	9.474	0.001
Cl4	0.590	0.061	0.640	0.007
H3	1.261	0.029	2.749	0.001
H9	1.200	0.031	1.160	0.001
H10	0.750	0.018	1.088	0.001
R4a	0.714	0.051	1.016	0.006
F1	3.021	0.007	12.574	0.000
F6a	0.667	0.027	0.875	0.001
F13	1.556	0.017	5.404	0.001
F19	0.412	0.015	0.381	0.000
T6	0.611	0.014	0.719	0.000
T8	0.600	0.022	0.927	0.001
T9	0.772	0.039	1.217	0.003
T8a	1.076	0.036	2.178	0.002
T9a	0.826	0.039	1.563	0.003
T10	1.536	0.021	4.182	0.001
T10a	1.886	0.024	6.678	0.001
T10b	0.937	0.014	1.823	0.000

(FA1) were registered in the length dimensions and in the upper epiphysis of the femur; lower values were registered in the diaphyseal and epiphyseal metric characteristics. However, after relating the FA size to the trait size (FA2 and FA6) the result was minimal, as in the upper limb.

The analyses comparing statistical differences of DA and FA in both populations revealed some interesting findings. In both types of asymmetry it was remarkable that among traits with significantly different levels of asymmetry, a majority (70% in DA and 75% in FA) had lower values of asymmetry in the medieval population. As some studies connect a greater level of asymmetry with increased environmental stress (Van Valen, 1962; Palmer, 1994; De Leon, 2007), our results support the theory that the Great Moravian population

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Table 7. Asymmetry differences (DA and FA) between recent and medieval populations

FA				DA			
Dimension	<i>U</i>	<i>P</i>		Dimension	<i>U</i>	<i>P</i>	
Males + Females							
H9	871	0.013*	rec	Cl5	7226	0.021*	rec
U1	2180.5	0.028*	rec	H9	930.5	0.025*	rec
R1	2581	0.057	rec	U11	7538.5	0.023*	rec
R4	5620	0.057	rec	F7a	8306	0.001**	rec
F13	4206	0.054	rec	F7c	7558.5	0.017*	med
T1	2757	0.054	rec	F7d	7036.5	0.031*	rec
T8	5458	0.047*	rec	F7e	6396.5	0.001**	med
T10a	5971	0.021*	med	Fi1	382	0.031*	rec
				T1	2718	0.040*	rec
				T1b	1610.5	0.030*	rec
Males							
F13	741.5	0.003**	rec	H5	2732.5	0.019*	rec
F19	496	0.005**	rec	U11	1406	0.016*	rec
T6	120	0.040*	rec	F7a	1373.5	0.000***	rec
T9	962.5	0.013*	rec	F7b	1406	0.003**	rec
F7e	1414	0.051	rec	F7e	1296	0.010**	med
				F9	1550.5	0.001**	rec
				T1	403	0.029*	rec
Females							
F9	2072	0.006**	med				
T10a	1856.5	0.012*	med	H10	859.5	0.039*	rec
U1	614	0.054	rec	F7e	1862	0.037*	med

Results of Mann-Whitney *U* test of males, females and both sexes, from both populations.

P significance levels:

* = 5%.

** = 1%.

*** = 0.1%.

was not subjected to highly stressful conditions. The previous multiple studies dealing with various features of this medieval population can serve as suitable information for comparison. Generally, the outcomes indicated that groups of the medieval population were healthier and subjected to less developmental perturbations than some of the more recent populations. One of the studies concentrated on osteoporotic changes on the proximal part of the femur in the Great Moravian population by means of double energy roentgen absorptiometry (DXA). Osteoporosis is a multifactor disorder caused also by insufficient nutrition. In an advanced state of osteoporosis, other conditions associated with loading appear – especially fractures (collum of femur). According to the average bone density (BMD) values, the early medieval population appeared to have better environmental living conditions than the recent population (Velemínský *et al.*, 2005b). These results supported surprisingly very low

occurrences of traumatic changes in skeletons of the Great Moravian population. This fact also indicates the good health status of individuals from this population (Likovský & Velemínský, in press).

The more marked FA in the recent population also confirms the results of sexual dimorphism where more expressed differences were found between sexes in the medieval population (Fialová, 2004; Žaloudková, 2004); a high degree of sexual dimorphism is considered to be a sign of good health and low environmental stress (Lazenby, 2002). Also, a previous study dealing with teeth features of the recent sample showed very bad health of teeth in relation to living conditions (Stránská *et al.*, 2005). Similarly, the height of stature and the overall gracility of skeletons of the recent sample (Fialová, 2004; Žaloudková, 2004) indicated a low quality of living conditions. Accordingly, the recent group from a lower social class (Pachner, 1937) was subject to higher

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environmental stress than the group from the Great Moravian period.

In general, it is asserted that individuals with right-hand dominance have a better developed right upper limb (Ruff & Jones, 1981). Therefore, all groups were divided according to their longest humeral length into hypothetical 'right-handers' (longer right humerus), 'left-handers' (longer left humerus), and 'ambidextrous' (both humeri of equal length) (*inter alia*, according to Steele & Mays, 1995; Čuk *et al.*, 2001) and their percentages were compared. In the recent population, 81.2% of males and 81.6% females had a longer right humerus, 12% of males and 13.6% of females had a longer left humerus, and 6.8% of males and 4.8% of females had both humeri of equal length. Our results correspond with the following investigations: Annett & Kilshaw (1983; 82% right-handers, 15% left-handers, and 3% of persons without a preference for any side), Steele & Mays (1995; 81% right-handers, 16% left-handers, and 3% of persons without a preference for any side), Čuk *et al.* (2001; 87% longer right humerus, 10% longer left humerus, and 3% both bones equally long). It is possible that the most asymmetric bone – the humerus – reflects a hand preference in this sample.

The results for the medieval population were different; 95.8% of males and 73.3% of females had a longer right humerus, 4.2% of males and 20% of females had a longer left humerus, and 6.7% of females and no males had both bones of equal length.

Conclusions

Considering the outcomes analysed in this study, asymmetry is confirmed to be a useful source of information when dealing with population characteristics based on anatomical structures and their differences. The highest frequency and level of DA registered in the upper limb bones, especially the humerus. As for FA, it was recorded in particular in the lower limb bones. These findings support the idea that the upper limb is subjected to biomechanical stress due to its strong asymmetrical use during life. Conversely, in the lower limb, the load that comes particularly from

'symmetrical' walking has a less conspicuous effect on the development of asymmetry.

FA is commonly used as a bioindicator of developmental stability, health and fitness of various populations. Although asymmetry in the human body, especially in limb bones, has been a recurrent subject of research, little effort was made to measure FA. The current study addresses FA in the context of human limb bones and considers the effects of environmental stress. In a comparison of two related samples under differential levels of health and environmental stress (Great Moravian population from the 9th–12th centuries, and a recent population from the first half of the 20th century), FA and DA were found to be relatively higher in the recent sample which was subjected to a higher level of stress.

In conclusion, we propose that bilateral asymmetry observed in diachronic skeletal populations of Central Europe showed some differences between them and can be used as an indicator of their biomechanical and environmental stress.

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Příloha D

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Three-dimensional geometric morphometric analysis of cranio-facial sexual dimorphism in a Central European sample of known sex

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ABSTRACT

This article presents an approach for estimating the sexual dimorphism of adult crania using three-dimensional geometric morphometric methods. The study sample consisted of 139 crania of known sex (73 males and 66 females) belonging to persons who lived during the first half of the 20th century in Bohemia. The three-dimensional co-ordinates of 82 ecto-cranial landmarks and 39 semi-landmarks covering the midsagittal curve of the cranial vault were digitised using a MicroScribe G2X contact digitiser. The purposes of the investigation were to define the regions of the cranium where sexual dimorphism is most pronounced and to investigate the effectiveness of this method for determining sex from the shape of the cranium. The results demonstrate that it is better to analyse apportionable parts of the cranium rather than the cranium as a whole. Significant sexual differences (significance was determined using multivariate analysis of variance) were noted in the shape of the midsagittal curve of the vault, upper face, the region of the nose, orbits, and palate. No differences were recorded either in the shape of the cranium as a whole or in the regions of the base and the neurocranium. The greatest accuracy in determining sex was found in the region of the upper face (100% of study subjects correctly classified) and the midsagittal curve of the vault (99% of study subjects correctly classified).

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Introduction

The existence of sexual dimorphism of the skeleton and its evaluation represent a presumption on which scientists base current methods for sex determination of a human skeleton (Rösing et al., 2007). Sexual dimorphism results in part from differing reproductive roles of the sexes and the strong selection pressure to which humans have been exposed throughout evolution. The degree of sexual dimorphism is influenced by environmental factors and thus differs in each population, though, on average, males are always larger, have more robust joints, and have a stronger musculature than females. Although sexual diagnosis is more accurate and reliable when based on the pelvis (Brůžek and Murail, 2006), the often poor state of pelvic preservation necessitates use of the cranium for the assessment.

An objective, quantitative approach to the study of sexual dimorphism is represented by conventional classification techniques of univariate and multivariate statistics. This approach uses measurements (distances, angles, or distance ratios) (Birkby, 1966; Boulinier, 1968; Giles, 1964; Giles and Elliot, 1963; Hanihara, 1959; Henke, 1974). These methods are based on observation of differences in the size of the skeleton, and any proposed discriminant function analyses are population specific. This is accentuated in recent forensic anthropology reports (Barrio et al., 2006; Bidmos, 2006; Bidmos and Dayal, 2004; Franklin et al., 2005; Frutos, 2005; Gualdi-Russo, 2007; Kemkes-Grotenthaler, 2005; Purkait and Chandra, 2004; Rösing et al., 2007; Šlaus et al., 2003). The quantitative approach to sex determination is also considered when studying skeletal samples derived from archaeological sites (Brůžek and Velemínský, 2006; Özer et al., 2006; Wrobel et al., 2002).

The accuracy of methods based on sexual dimorphism of the cranial measurements will diminish when these methods are used outside the reference population. Using population-specific methods or national standards with respect to the size of the skeletons (İşcan, 1988) is not a solution, as useful collections of skeletons of known age and sex are not available for every population. Body size has changed through generations of the same population as a consequence of secular trend (Jantz, 2001; Jantz and Jantz, 1999; Klepinger, 1999; Meadows and Jantz, 1995). Thus, it may be assumed that methods for determining sex, in which measurements obtained from collections of skeletons of known sex from the first half of the 20th century, are used, cannot guarantee the same reliability of results when they are used in attempt to identify unknown human remains from recent populations. This disadvantage could be eliminated by using re-scaling three-dimensional geometric morphometrics (3D GM). Although visual (qualitative) methods of sex determination are mostly not population specific and are relatively simple and accurate (Williams and Rogers, 2006), their use requires a lot of training and their application is subjective. The problems presented by both of these approaches have been well documented by Bookstein et al. (1985) and Slice (2005, 2007).

Geometric morphometrics represents a new approach in the evaluation of variability, not only in the biomedical disciplines but also in such areas as bioarchaeology, evolution, and ecology. The term geometric morphometrics, which was first used by Corti (1993), includes methods based mainly on 3D co-ordinates of homologous landmarks that describe the studied object. The co-ordinates thus represent complete geometric information related to the studied object (Slice, 2007). When analysing the forms of biological objects, GM enables differentiation of variability due to both size and shape. Quantification of shape and size using statistical GM procedures specifies and renders more accurate results than those that have been obtained to date with other methods, thus increasing their reliability (Bookstein, 1991; Dryden and Mardia, 1998; Richtsmeier et al., 2002; Rohlf, 2003; Slice, 2007).

The most frequent applications of geometric morphometrics in forensic anthropology relate to determination of population affinity or ancestry (Buck and Vidarsdottir, 2004; Ross et al., 1999), assessment of age at death (Braga and Treil, 2007), and determination of sex (Franklin et al., 2006a,b, 2007b, 2007c; Kimmerle et al., 2008; Oettlé et al., 2005; Pretorius et al., 2006; Ross et al., 2006; Steyn et al., 2004). GM methods are not intended to replace methods currently used for sex assessment. Rather, their aim is to quantify shape and characterise shape variability and, in doing so, to evaluate objectively any differences in shape and compare them with other variables while preserving all of the geometric information corresponding to the original object (Slice, 2005).

The current economic globalisation and the associated movement of people require that methods of sexual determination used in forensic anthropology take these facts into consideration as seriously as in the case of age estimation (Schmeling et al., 2001). This means that the methods for determining sex should not be population specific but should, if possible, be both accurate and reliable.

The aim of our study was to analyse the sexual dimorphism of crania from the Central European population and to verify whether sex can be determined using shape characteristics of the cranium. Another task was to locate the regions of the cranium where sexual dimorphism was most pronounced. We believed that comparison of the results of a North American sample (Kimmerle et al., 2008) and a South African population (Franklin et al., 2006a, 2007a) with a Central European population would show whether sexual dimorphism of cranial shapes demonstrates logical homology in various populations.

Material

A series of 139 adult crania of known age and sex from the Central European population, from the so-called Pachner collection housed in the Department of Anthropology and Human Genetics, Faculty of Science, Charles University, Prague, has been used for this study. Among the 139 crania, all without significant pathology, 73 were male of ages ranging from 20 to 96 years (average age 51 years) and 66 were female crania ranging in age from 20 to 91 years (average age 53 years).

The collection originated in the 1930s with the intent of studying the sexual dimorphism of the human skeleton (Borovanský, 1936; Pachner, 1937). According to Pachner (1937), the material came from inhabitants of Bohemia, mainly from lower socioeconomic classes. During the second half of the 20th century this collection was often used for studying and revising methods for sex determination (e.g. Černý and Komenda, 1986; Novotný, 1986; Novotný et al., 1993; Strádalová, 1972).

Methods

Data acquisition

To answer *a priori* questions of sexual dimorphism of the cranial shape, we chose 82 ecto-cranial anatomical landmarks (Martin and Saller, 1957) that provided a high level of anatomical detail of 7 regions (the configuration of neurocranium, cranial base, midsagittal curve of vault, upper face, orbital region, nasal region, and palatal region). The chosen landmarks were precisely defined and could be located unambiguously, thus were repeatable. To adequately represent the cranium as a whole, we chose crania on which the landmarks were as widely distributed as possible (Rohlf, 1996; Snow, 2004; Table 1).

Because only a few landmarks were available on the brain vault, it was digitised as the midsagittal curve (from the *nasion* to the *opistion*) on the external neurocranial surface as a series of discrete points—39 semi-landmarks. It should also be noted that no landmarks around alveolar processes were used for analysis, because of frequent intravital loss of the anterior teeth.

All landmarks and the curve in the midsagittal plane were recorded in three dimensions using a MicroScribe G2X contact digitiser (Immersion Corp., San Jose, CA, USA). Each cranium, fixed in plasticine, was digitised in two positions (DeLeon, 2004). The first position with the cranium resting on its base enabled the recording of almost all landmarks chosen in the region of the face and vault. The remaining landmarks, especially on the *basicranium*, were then acquired with the cranium resting on its vault. In both positions, three reference points (*bregma*, *nasion* and *lambda*) were marked on each cranium as the origin and x- or y-axis directions. These points were used to align all landmarks of each cranium within a common co-ordinate system. The combination of the superior and inferior aspects provided a complete configuration.

Table 1
List of landmarks.

No.	Abbreviation	Landmark	Use of Landmarks in Studied Regions of Skull	Definition
<i>Midline Cranial Points</i>				
1	b	<i>bregma</i>	Va	Intresection of the <i>sut. coronalis</i> and <i>sut. sagittalis</i> in the midsagittal plane
2	ns	<i>nasion</i>	NsR, UpF	The middle of the <i>sut. nasofrontalis</i> in the midsagittal plane
3	l	<i>lambda</i>	Va	Intersection of the <i>sut. sagittalis</i> and <i>sut. coronalis</i> in the midsagittal plane
4	rhi	<i>rhinion</i>	NsR	The lowest point of the <i>sut. internasalis</i>
5	ns	<i>nasospinale</i>	NsR, UpF	Intersection of the subtence/chord inferior margins of the <i>apertura piriformis</i> and the midsagittal plane
6	pr	<i>prosthion</i>	Pl	The most prominent point in the midsagittal plane between the upper incisors
7	o	<i>opisthion</i>	Ba, Va	The midpoint of the posterior margin of the <i>foramen magnum</i> in the midsagittal plane
8	ba	<i>basion</i>	Ba, Va	The midpoint of the anterior margin of the <i>foramen magnum</i> , opposite the opisthion.
9	ho	<i>hormion</i>	Ba	Intersection of the midsagittal plane and the line where the base of <i>vomer</i> meets <i>os sphenoidale</i>
10	sta	<i>staphylion</i>	Pl	The point where subtence/chord of posterior margin of the palate intersects the midsagittal plane
11	sr	<i>staurion</i>	Pl	Intersection of the <i>sut. palatina mediana</i> and <i>sut. palatina transversa</i>
12	inc	<i>foramen incisivum</i>	Pl	The point on the posterior margin of the <i>foramen incisivum</i>
<i>Bilateral Cranial Points</i>				
13&14	ast	<i>asterion</i>	Va	Intersection of the <i>sut. lambdoidea</i> , <i>sut. parietomastoidea</i> and <i>sut. occipitomastoidea</i>
15&16	ent	<i>entomion</i>	Va	The point, where the <i>sut. squamosa</i> passes into <i>sut. parietomastoidea</i>
17&18	k	<i>crotaphion</i>	Va	Intersection of the <i>sut. sphenosquamosa</i> , <i>sut. sphenoparietalis</i> and <i>sut. squamosa</i>
19&20	sphn	<i>sphenion</i>	Va	Intersection of the <i>sut. coronalis</i> , <i>sut. sphenoparietalis</i> and <i>sut. sphenofrontalis</i>
21&22	eu	<i>euryon</i>	Va	The extremity, on either side, of the greatest transverse diameter of the skull
23&24	co	<i>coronale</i>	Va	One of the two most widely separated points on the <i>sut. coronalis</i> at the poles of the greatest frontal diameter
25&26	ft	<i>frontotemporale</i>	UpF, Va	The most anterior point of the <i>linea temporalis</i> on the <i>os frontalis</i>
27&28	au	<i>auriculare</i>	Va	Intersection of the base of zygomatic arch and the midline of the opening of the <i>meatus acusticus externus</i>
29&30	zts	<i>zygotemporale superior landmark x</i>	UpF	The most superior point on the <i>sut. zygomaticotemporalis</i>
31&32	x	<i>landmark x</i>	Va	Intersection of the <i>sut. sphenozygomatica</i> , <i>sut. sphenofrontalis</i> and <i>sut. frontozygomatica</i>
33&34	ju	<i>jugale</i>	UpF	The point at the union of the <i>processus frontalis</i> and <i>processus temporalis</i> of the <i>os zygomaticus</i>
35&36	zy	<i>zygion</i>	UpF	The most lateral point of the zygomatic arch
37&38	apt	<i>apertion</i>	NsR, UpF	The most lateral point on the nasal aperture
39&40	fmt	<i>frontomalare temporale</i>	UpF	The most posterior/lateral point on the <i>sut. frontozygomatica</i>
41&42	fmo	<i>frontomalare orbitale</i>	Or, UpF	Intersection of the <i>sut. frontozygomatica</i> and the lateral margin of the orbit
43&44	mnf	<i>maxillonasofrontale</i>	NsR, UpF	Intersection of the <i>sut. frontonasalis</i> , <i>sut. frontomaxillaris</i> and <i>sut. nasomaxillaris</i>

Table 1 (continued)

No.	Abbreviation	Landmark	Use of Landmarks in Studied Regions of Skull	Definition
45&46	mf	<i>maxillofrontale</i>	Or, NsR, UpF	Intersection of the <i>sut. frontomaxillaris</i> and the medial margin of the orbit
47&48	ek	<i>ectoconchion</i>	Or, UpF	Intersection of the lateral margin of the orbit and the line from the <i>mf</i> parallel with the superior margin of the orbit
49&50	spa	<i>supraconchion</i>	Or, UpF	Intersection of the superior margin of the orbit and normal to the line <i>mf-ek</i>
51&52	sbk	<i>subconchion</i>	Or, UpF	Intersection of the inferior margin of the orbit and normal to the line <i>mf-ek</i>
53&54	zti	<i>zygotemporale inferior</i>	UpF	The most inferior point on the <i>sut. zygomaticotemporalis</i>
55&56	zm	<i>zygomaxillare</i>	UpF	The most inferior point on the <i>sut. zygomaticomaxillaris</i>
57&58	io	<i>infraorbitale</i>	Ba, UpF	The most lateral point on the margin of the <i>foramen infraorbitale</i>
59&60	ms	<i>mastoidale</i>	Ba, Va	The most inferior point on the <i>processus mastoideus</i>
61&62	basty	<i>basostyloidion anterior</i>	Ba	The most anterior point on the base of the <i>processus styloideus</i>
63&64	fol	<i>foraminolaterale</i>	Ba	The most lateral point on the margin of the <i>foramen magnum</i>
65&66	laco	<i>occipitocondylion laterale</i>	Ba	The most lateral point on the margin of the <i>condylus occipitalis</i>
67&68	meco	<i>occipitocondylion mediale</i>	Ba	The most medial point on the margin of the <i>condylus occipitalis</i>
69&70	antco	<i>occipitocondylion anterior</i>	Ba	The most anterior point on the margin of the <i>condylus occipitalis</i>
71&72	poco	<i>occipitocondylion posterior</i>	Ba	The most posterior point on the margin of the <i>condylus occipitalis</i>
73&74	cam	<i>caroticum mediale</i>	Ba	The most medial point on the margin of the <i>foramen caroticum externum</i>
75&76	ovm	<i>ovale mediale</i>	Ba	The most medial point on the margin of the <i>foramen ovale</i>
77&78	spi	<i>spinale</i>	Ba	The most medial point on the margin of the <i>foramen spinosum</i>
79&80	poa	<i>postalverion</i>	Pl	The most posterior point on the <i>processus alveolaris</i> of the <i>maxilla</i>
81&82	it	<i>infratemporale</i>	Ba, Va	Intersection of the <i>sut. sphenosquamosa</i> and <i>crista infratemporalis</i> of the sphenoid bone

Use of Landmarks in Studied Regions of Skull:

Or—Orbits; NsR—Nasal Region; Pl—Palate; Ba—Base; UpF—Upper Face; Va—Vault.

Precision of measurement

All landmarks and semi-landmarks of six specimens were digitised six times, with a minimum of 1 day allowed between digitisation to assess the degree of intra-observer error in data acquisition. The six repeated sets of co-ordinates were submitted to generalised Procrustes analysis (GPA) and principal component analysis (PCA) along with the total sample, in accordance with the method used by O'Higgins and Jones (1998), and Franklin et al. (2006a, 2007b).

Shape analysis

Using GPA, raw landmark co-ordinates were re-scaled, translated, and rotated for elimination of nonshape variation in the sample. For each cranium, the centroid size was calculated and used in subsequent statistical analysis (Bookstein, 1991, Dryden and Mardia, 1998). Multivariate analysis of variance (MANOVA) was used to assess the significance of sexual differences in the sample.

Procrustes residuals were analysed using PCA, which explores the relationships between the population means of male and female crania. Because size had effectively been removed from the analysis, the PCA was more sensitive to subtle shape differences, spread over a large number of principal components (PCs) (Franklin et al., 2006a). The PCA scatterplot visually represented the variation among different individuals of the sample. The mean shape of the sample was situated where the PCs crossed. The associated shape variations were visualised and explored using wire-frame models. The thin-plate spline (TPS) provided an exact mapping of the landmarks of one configuration onto another and supplied a maximally smooth interpolation of the interlandmark space (Slice, 2007). TPS was used to show deformation of shape using Cartesian grids to visualise which landmarks were responsible for the differences in shape between PC extremes. Discriminant function analysis was performed to assess the sex classification accuracy of the discriminant functions (Davis, 1986; Franklin et al., 2006b).

Statistical analysis was performed using the following software programs: Morphologika for TPS and PCA (<http://www.york.ac.uk/res/fme/resources/software.htm>) (O'Higgins and Jones, 2006), PAST for discriminant function analysis (<http://folk.uio.no/ohammer/past>) (Hammer et al., 2001), and Morphueus et al. for MANOVA (www.morphometrics.org/morpheus.html) (Slice, 1998).

Results

Intra-observer variation of the landmark positions was tested using six repetitions of six specimens (two females and four males) clustered closely together on PCs 1 through 10. The first two PCs are plotted in Fig. 1. This indicates that errors of precision of measurement were small with respect to sample variability and were unlikely to have unduly influenced the results.

Initially, we focused on determining sexual dimorphism of the entire shape of the cranium. The preservation of the crania and thus the number of possible landmarks was a significantly limiting factor that decreased the number of individuals in the sample. We did not find any sexual differences in whole crania in our sample. Nonetheless, the presence of partial shape differences drew our attention to areas of the cranium on which to focus our subsequent steps. When we monitored shape

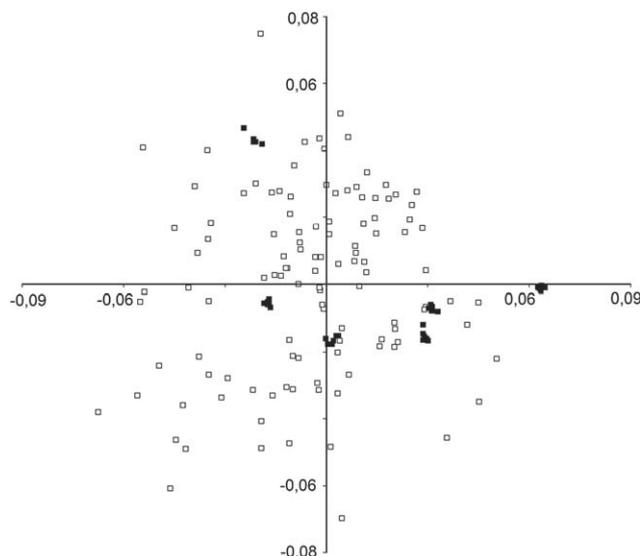


Fig. 1. Precision of measurement: Principal component (PC) 1 (horizontal axis) accounts for 14.9% and PC2 (vertical axis) for 13.4% of the total variance in the sample. In this chart, the six instances of each test specimen (five repeats plus one original) are plotted in black. The other specimens (one set of measurements from each) are plotted as open symbols.

Table 2
Results of MANOVA

Region	Number of Landmarks	MANOVA		% Correctly Classified (n)	
		p	Total	Male	Female
Upper Face	32	0.002 ^b	100.000	100.000 (67 of 67)	100.000 (58 of 58)
Nasal Region	9	0.002 ^b	77.120	77.400 (48 of 62)	76.800 (43 of 56)
Orbits	10	0.002 ^b	74.440	70.800 (51 of 72)	78.700 (48 of 61)
Palate	6	0.006 ^b	70.410	71.200 (37 of 52)	69.600 (32 of 46)
Midsagittal Curve	41	0.024 ^a	99.260	100.000 (73 of 73)	98.400 (62 of 63)

MANOVA, multivariate analysis of variance.

^a 5% level of statistical significance.

^b 1% level of statistical significance.

dimorphism of seven specific regions of the cranium, the size of the sample increased from $n=98$ to $n=136$. Among these regions, the area of the cranium base and the neurocranium configuration did not demonstrate significant sexual dimorphism. We have therefore limited the subsequent presentation of our results to those regions where we noted significant differences between the sexes: the midsagittal curve, the upper face, the orbital region, the nasal region, and the palatal region. All five selected regions demonstrated strong sexual dimorphism.

The results of MANOVA and discriminant function analysis are presented in Table 2.

The midsagittal curve of the neurocranium

For assessing sexual dimorphism on the midsagittal curve of the vault, a total of 41 landmarks (the *nasion*, *opisthion*, and 39 semi-landmarks between them, which cover the midsagittal curve) and 136 crania were tested (females, 63; males, 73). MANOVA showed significant differences between sexes in this region ($p=0.02$).

The PCA showed that PC4 represented the part of shape variability that is most responsible for sexual differences (Fig. 2). Fig. 3 shows the shape changes visualised by morphing from the negative (female) to positive (male) extreme of PC4.

Females had a more spherical neurocranium. The *bregma* region was found to be relatively higher in males than in females. Males had a more posteriorly projecting occipital plane; the frontal region was flatter and the *glabella* more prominent. Females had a more rounded forehead, flatter *bregma* region, and a rounded occipital region. In females, a relatively shorter distance between the *nasion* and *opisthion* points was noted.

Discriminant analysis showed 99% accuracy of sex determination (females, 62 of 63; males, 73 of 73) when using landmarks on the midsagittal curve (Table 2, Fig. 4).

The upper face

Significant sexual dimorphism was found (MANOVA t -test: $p=0.002$) when using 32 landmarks on the upper face region in a sample of 125 specimens (females, 58; males, 67). The PC most responsible for sexual dimorphism in the shape of the upper face was PC4, which accounted for 7% of the total shape variance of the sample.

As illustrated in Fig. 5, males had a relatively lower and wider face than females. In general, males exhibited relatively flatter and more vertical upper face and relatively wider and higher zygomatic arches in the upper part of the face. In contrast, females in the sample typically had a relatively higher forehead and face. Viewed from above, females had a more convexly shaped face compared with a flatter profile among males.

A more detailed frontal view shows that females had a relatively parallel *ft-ju* line, whereas in males, the *jugale* points were relatively further apart. (See Table 1 for definitions of landmark

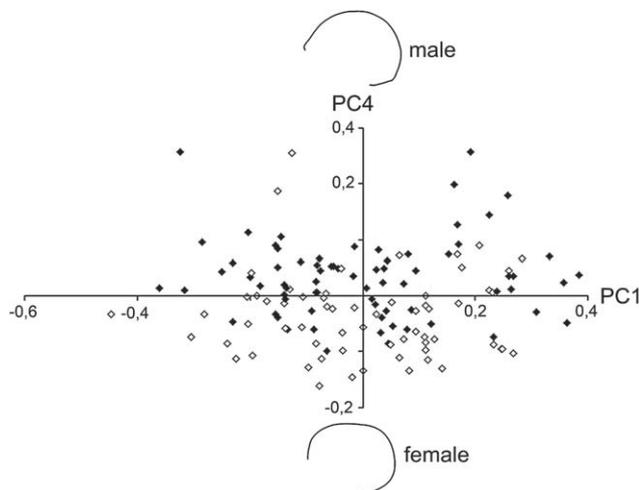


Fig. 2. Principal component analysis of the shape variance on the midsagittal curve of the neurocranium. Principal component (PC) 1 accounted for 32.2% of the total shape variance of the sample versus PC4, which accounted for 7.1%. $N=136$; 41 landmarks. PC4 separated the two sexes. Lateral views of the midsagittal curve show the variation in cranial shape represented by PC4. Males, solid-black symbols; females, open symbols.

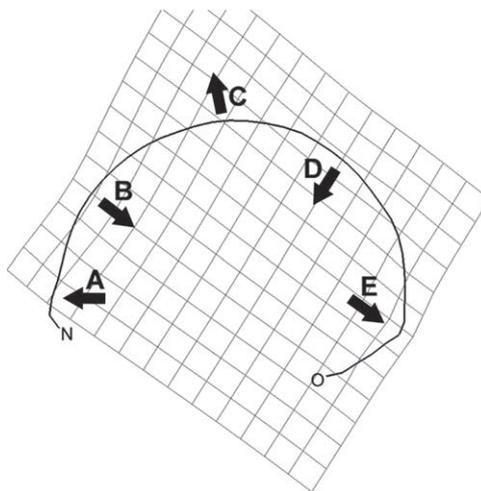


Fig. 3. The thin-plate spline grid shows the variation in shape of the midsagittal curve of the vault represented by PC4 (sexual differences; female \rightarrow male). Reference shape is represented by "female," target shape by "male." (A) protrusion of the *glabella* region; (B) flattening of the frontal region; (C) vaulting of the *bregma* area; (D) flattening of the *lambda* region; (E) acute angle of the *inion*.

abbreviations.) Compared with females, males had a relatively shorter distance between the *frontotemporale* and the *fmo* and *fnt* points, as well as a shorter height of the nasal region. Overall, males had relatively wider zygomatic arches and more distant *zygion* points, whereas the *zygomaxillare* points were relatively closer and the angle *zm-io-apt* was more obtuse than in females. A detailed view from above shows a more vertical upper face and orbit in males. In females, the *subconchion* jutted more anteriorly and the *supraconchion* shifted posteriorly. Similarly, the *frontotemporale* shifted more posteriorly compared with the *fnt* and *fmo*. The *nasospinale* in males

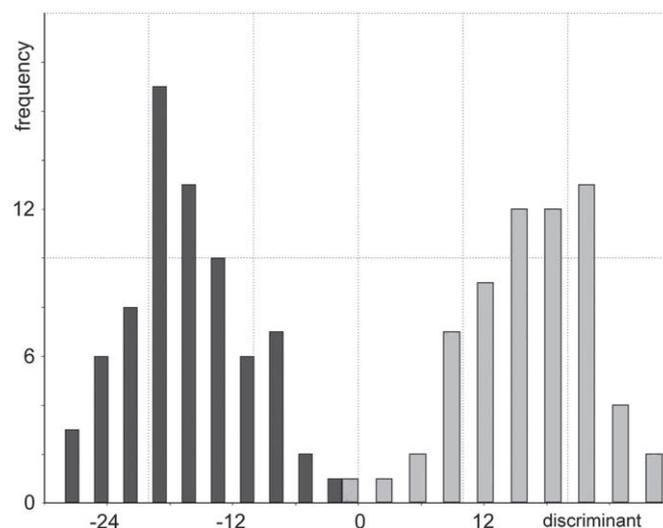


Fig. 4. A graph of the results of discriminant analysis conducted on the midsagittal curve of the vault. Negative values of the discriminant—males, positive—females. One female was classified as a male.

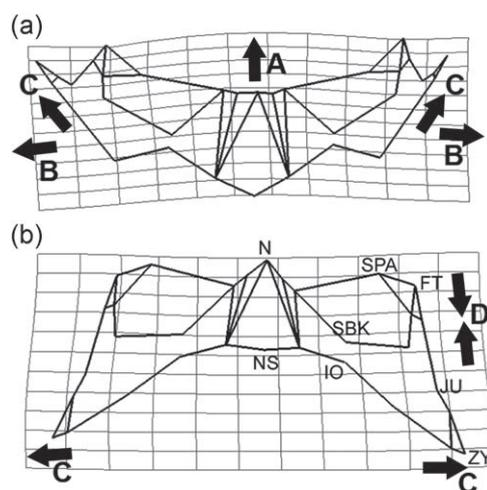


Fig. 5. The thin-plate spline grid shows the variation in the shape of the face represented by PC4 (sexual differences; female → male). Reference shape is represented by “female,” target shape by “male.” (a) superior view; (b) frontal view. (A) antero-posterior flattening of the face, shifting of the maxilla posteriorly; (B) relative widening of the face; (C) wider zygomatic arches; (D) relative lowering of the face. See Table 1 for definitions of landmark abbreviations.

jutted relatively more to the front than in females. In this view, females had a more acute facial angle; for example, in the angle *zy-n-zy*, the points *zy-zy* were relatively closer to each other. The lateral view shows that the *frontotemporale* was significantly shifted anteriorly in males, whereas the distance of *frontotemporale* from the *fmo* and *fnt* points was shorter. The angle *zy-ju-fnt* in males was more obtuse than in females, and the *zti-zts* line was more vertical to the base (in females, *zts* projected more forward, and *zti*, more backward than in males). *Nasospinale* and *nasion* in males shifted more anteriorly and *maxillonasofrontale* and *maxillofrontale*, more posteriorly.

The sexing accuracy for the region of the upper face was 100% (females, 58 of 58; males, 67 of 67).

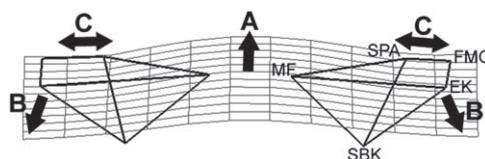


Fig. 6. The thin-plate spline grid shows the variation in shape and space orientation of orbits represented by PC4 (sexual differences; female→male). Reference shape is represented by “female,” target shape by “male.” (A) posterior shift of the medial landmarks; (B) anterior shift of lateral landmarks; (C) relative widening of the orbit. See Table 1 for definitions of landmark abbreviations.

Orbital region

When analysing landmarks on the orbits (133 crania: 61 females and 72 males; 10 landmarks), MANOVA showed significant differences between sexes ($p=0.002$). The PCA showed that the PC4 (8.6% variability) was most responsible for the sexual differences of the shape and spatial orientation of the orbits.

Compared with the more rounded orbit in females (Fig. 6), in males the orbit was relatively lower and wider. The *aditus orbitae* (orbit aperture) of males was parallel to the frontal plane; in females it was positioned in a slightly sagittal direction. In females, the orbit medial landmarks (*maxillofrontale*) shifted more anteriorly and the lateral landmarks (*ectoconchion* and *frontomolare orbitale*) more posteriorly when compared with males. The frontal view shows that in females, the line connecting *mf-ek* was almost horizontal with respect to the base, while in males the *maxillofrontale* had a higher location.

The accuracy of sex determination for the region of the orbit was 74% (females, 48 of 61; males, 51 of 72).

The shape of the nasal region

The sexual dimorphism of the nasal region was assessed with the help of 9 landmarks in a sample of 118 crania (56 females, 62 males). The results of MANOVA showed significant differences between sexes ($p=0.002$). The PC most responsible for the sexual differences of the shape of this region was PC3 (11.2% variability).

In males, the nasal aperture was relatively higher and narrower, with a deeper nasal base (*nasion* and *maxillonasofrontale* deeper but widely spaced apart), and the nasal bones were more prominent. In females, the nasal bones (and also the base of the nose) were flatter, the nasal aperture was relatively wider, and the orbits were relatively farther apart than in males (Fig. 7). The frontal view shows that in males the *maxillonasofrontale* and *maxillofrontale* were relatively higher and closer together than in females. In females, the *rhinion* was located relatively lower. The view from above shows that the *apt-n-apt* angle was more acute in males, whereas in females it was almost 180° .

The sexing accuracy for the region of the upper face was 77% (females, 43 of 56; males, 48 of 62).

The shape of the palate

For the assessment of sexual dimorphism of the palate, a total of 98 crania (females, 46; males, 52) and 6 landmarks were analysed using MANOVA, and significant differences between sexes were found ($p=0.006$). PCA showed that PC3 most significantly distinguished the two sexes (18.7% variability).

The *prosthion* projected more anteriorly relative to the rest of the cranium in females when compared with males. Females had a relatively lower and wider palate compared with males, who had a deeper and narrower palate (Fig. 8). The view from above shows that in females, the *staphylion* and *staurion* are closer to each other than in males. Using the frontal view, we noted that the *poa-sr-poa* angle was nearly flat.

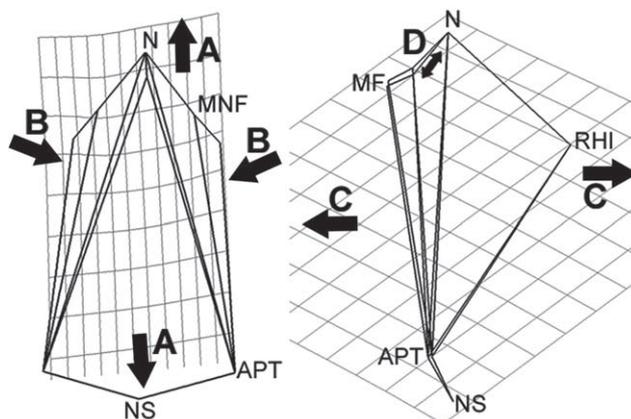


Fig. 7. The thin-plate spline grid shows the variation in shape of the nasal region represented by PC3 (sexual differences; female→male). Reference shape is represented by “female,” target shape by “male.” (A) relative elongation of the nasal aperture; (B) relative approximation of the orbits and relative narrowing of the nasal aperture; (C) greater prominence of the nasal bones; (D) nasion and maxillofrontale relatively more widely separated. See Table 1 for definitions of landmark abbreviations.

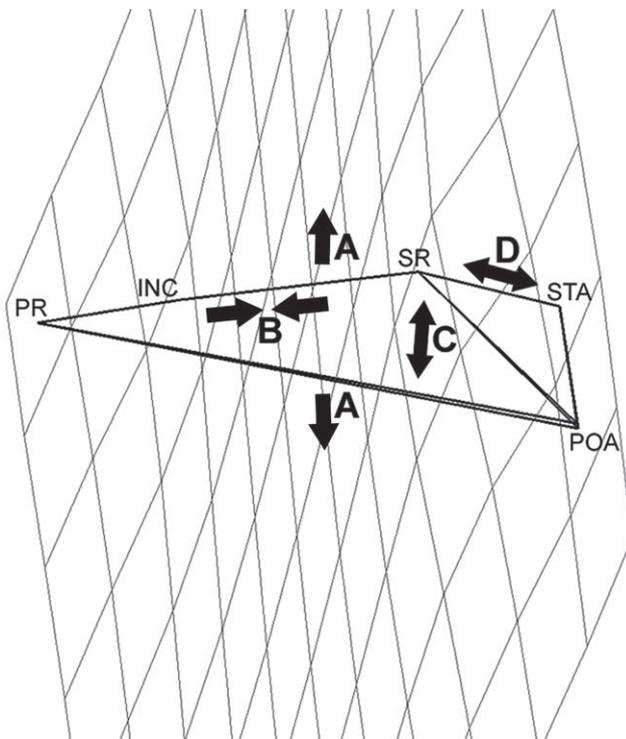


Fig. 8. The thin-plate spline grid shows the variation in the shape of the palate represented by PC3 (sexual differences; female→male). Reference shape is represented by “female,” target shape by “male.” (A) excavation of the palate region; (B) relative shortening of palate length; (C) excavation of the palate in the area of the sutura palatina transversa; (D) elongation of the posterior section of the hard palate. See Table 1 for definitions of landmark abbreviations.

The discriminant analysis showed 70% accuracy for sex determination (females, 32 of 46; males, 37 of 52) of the palate.

Discussion

Current difficulties of traditional sexing techniques

Determination of sex (sexing) is important in forensic sciences and archaeology (Brinkmann, 2007; Cattaneo, 2007; Graham, 2006). In sex determination, classical visual methods generally reach a sexing accuracy of about 90%. A set of morphologic traits of the cranium allow for accurate estimation of sex in 80% of cases, with a risk error of less than 10% (Williams and Rogers, 2006). However, in general, it is not suitable to rely on only one morphologic trait when estimating sex (Sjøvold, 1988). The application of logistic discriminant analysis models, thanks to the cranial trait scoring system, increases the accuracy of correctly classifying crania to 84% or even 88% (Walker, 2008). Even this approach, however, shows population specificity. The greatest problem in evaluating individual morphoscopic traits is the significant degree of subjectivity.

The advantage of traditional morphometric methods lies in their objectivity. Moreover, discriminant functions calculated on the basis of cranial measurements reach a high accuracy (85% to 95% of correctly classified individuals; Franklin et al., 2006a; Giles and Elliot, 1963; Howells, 1964; Steyn and İşcan, 1998). Morphometric methods are burdened by a classification error that ranges between 10% and 15% (Krogman and İşcan, 1986; Mays and Cox, 2000; Meindl et al., 1985), and up to 20% with crania (Masset, 1987; St. Hoyme and İşcan, 1989). The main problem of sexing forensic and archaeological material is the damage such material has incurred. Determination of sex with the help of dimensions from a single anatomic region of the cranium provides a lower, but still relatively high, success rate of classification (e.g. Gapert et al., 2009; Holland, 1986; Monticelli and Graw, 2008; Nagaoka et al., 2008; Wahl and Graw, 2001).

With cranium dimensions, however, size-related sexual dimorphism shows significant inter-population variability (e.g. Kemkes and Göbel, 2006). Both general robustness/gracility and the magnitude of sex-related differences (sexual dimorphism) depend on the particular regional population (Rösing et al., 2007). The application of discriminant functions on populations other than those for which they have been calculated leads to significant errors (e.g. Spradley et al., 2008). Sexual dimorphism of cranium size is also subject to demographic changes affecting population composition and the influence of secular trends. These findings are supported by studies of the North American population (e.g. Jantz, 2001) as well as of the Central European population (Buretić-Tomljanović et al., 2006; Jonke et al., 2007; Susanne et al., 1988). At the same time, the significant movement of residents, in connection with trade and tourism, prevents determination of the population specificity of an identified case with absolute certainty, and thus the application of population-specific methods is limited. Sex determination using the human cranium is generally based on size differences and robustness (Gapert et al., 2009). For these reasons, it is very important to determine whether it is possible to successfully determine sex using the shape of the cranium, after removing the size factor, the main variable in the population specificity of the methods.

Geometric morphometrics and sexual dimorphism of the cranium

GM present a possible solution to this problem (see above). According to Slice (2005), GM represents “the suite of methods for the acquisition, processing, and analysis of shape variables that retain all of the geometric information contained within the data.” The main contribution of GM to forensic anthropology lies in eliminating subjectivity from the evaluation of shape and the possibility of an objective proposal of categories for nonmetric standards of sexual dimorphic traits (Franklin et al., 2006a, 2007b; Pretorius et al., 2006). Moreover, GM methods also enable the quantification of regions lacking sufficient incidence of suitable landmarks with the aid of curves serving as contours that can be digitised to form a series of discrete landmarks, so-called semi-landmarks (Perez et al.,

2006). Another advantage of GM is its frequently higher classification accuracy when separating groups of crania according to sex, when compared with the traditional discriminant functional analysis of linear dimensions (Franklin et al., 2006a, 2007b). Authors describe a classification accuracy of 87% in methods using the cranium as a whole, which is more than in the case of traditional morphometric techniques (e.g., in the same population, the classification accuracy of linear dimensions was only 80%; Franklin et al., 2005).

It is well known that sexual dimorphism is expressed more distinctly, the better the living conditions and health status of the given population (Lazenby, 2001). Our series comes from a lower social class of the populace (Pachner, 1937), which has been confirmed by studies that monitored the condition of dentition (Stránská et al., 2005), or the asymmetry and robustness of the skeleton (Fialová, 2004; Kujanová et al., 2008; Žaloudková, 2004). In such collections, it is useful to use 3D GM methods, which enable detection of specific traits of sexual dimorphism, which cannot be distinguished using traditional visual or metric methods. This is also due to the fact that sexual dimorphism is moreover based on fundamental and unique changes of shape with imperceptible differences between populations and is not merely an issue of size (Kimmerle et al., 2008).

Geometric morphometrics and sexing

Our results show that geometric morphometrics are a suitable instrument for evaluating the sexual differences of crania. In the series studied, we attained 100% classification accuracy for both sexes in the case of the upper face, and 98% accuracy in females and 100% accuracy in males in the case of the midsagittal curve of the neurocranium. Such results fully meet the requirements of forensic practice for high accuracy and reliability in sex determination (Scheuer, 2002).

The success of sexual diagnosis depends not only on the method selected but also on the anatomic regions of the skeleton and the degree of sexual dimorphism of the given population. Three-dimensional methods of studying cranium variability have shown the importance of the shape component of the facial skeleton for describing the variability within and between various population samples (Bruner and Manzi, 2004; Hennessy and Stringer, 2002), as well as the cranium as a whole (Badawi-Fayad and Cabanis, 2007; Franklin et al., 2007b). Sexual differences in the cranium are evidently associated with the physical constitution and energy requirements (Rosas and Bastir, 2002); this applies especially to the area of muscle attachments. Examples include, for example, facial prognathism, the relative bizygomatic width, the degree of glabella development, the profile of the forehead, the development of the mastoid processes, and the shape of the occipital region (Franklin et al., 2006a; Hennessy et al., 2002).

According to Franklin et al. (2006a), relative bizygomatic width best determines the sex, followed by the shape and profile of the forehead and the face. Our results show that the best sex-discriminating region of the cranium is the shape of the upper face (females, 100%; males, 100%). We recorded the most significant sexual differences in the relative width and robustness of the zygomatic arches. In male crania, the upper face was both relatively lower, wider, flatter, and vertically oriented. Female crania had a more convexly shaped face when viewed from above.

Although the shape of the orbits is not a commonly used method for sex determination (Pretorius et al., 2006), we recorded significant sexual differences in the shape, mutual position, and spatial orientation of the orbits. Apart from the commonly described more oval orbit in females and the more angular (relatively longer and lower) orbit in males (Krogman and İşcan, 1986; Pretorius et al., 2006), we discovered differences in orbit orientation. The orbits of males were more or less parallel to the frontal plane, whereas those of females were oriented more in the sagittal direction. Such findings are possible only when using GM methods. Pretorius et al. (2006) were surprised by the percentage of correctly classified individuals, where 80.0% of females and 73.3% of males were classified correctly on the basis of orbit shape, these values being higher than those in the case of the shape of the mandibular arms in the same sample of South African crania. Our values (females, 78.7%; males, 70.8%) are somewhat lower, probably because of the generally lower sexual dimorphism of this Central European series. Nonetheless, it is clear that the area of the orbit identifies females better. The relatively high percentage of correctly classified individuals

demonstrates the appropriateness of using GM methods in forensic anthropology. Such claims are also supported, for example, by the fact that neither the distance and height of the orbit in this series (Hudcová, 2006) nor the distance of the orbits in the recent adult Czech population as calculated using radiographs (Šmahel et al., 1998) shows sexual dimorphism.

We conducted the analysis of the nasal region on the basis of uncovered nonsignificant sexual differences in the width of the nasal aperture, the length of nasal bones, and the height of the nasospinale-prosthion in this series of crania (Hudcová, 2006) and the length of the nasal bones on radiographs of the adult Czech population (Šmahel et al., 1998). This uncommonly used region is often limited by insufficient preservation. In the case of male crania, however, the nasal region surprisingly discriminated sex better than the orbital region did (females, 76.8%; males, 77.4%). Our results confirm, similarly to those of Franklin et al. (2006a), the more prominent nasal bones along with deeper nasion depression in males. Our study, moreover, describes a relatively longer and wider nasal aperture in male crania.

Significant sexual dimorphism was also noted in the area of the palate. Our results are consistent with the findings of Šmahel et al. (1998), whose studies were conducted using radiographs and 3D models of the palate of the adult Czech population, as well as with findings of the study of Franklin et al. (2006a) on the South African population. Females had a more prominent proclination of the upper alveolar process with respect to the level of the palate—or, in other words, males had a relatively shorter, deeper, and narrower palate.

Although significant sexual differences are described in the region of the cranium base using size and robustness (Gapert et al., 2009; Holland, 1986) as well as shape with the aid of GM (Bruner and Ripani, 2008; Franklin et al., 2006a), our study did not demonstrate any significant sexual dimorphism of the shape of the cranium base. In contrast to Franklin et al. (2006a), for example, we did not record any significant sexual dimorphism in the region of the neurocranium configuration either. The shape of the midsagittal curve represents an exception. The landmarks on the midsagittal curve of the vault, defining its shape, enabled us to achieve a surprisingly high classification accuracy of sexing (females, 98.4%; males, 100%), although another study using the same material (Hudcová, 2006) did not show significant sex-related differences in the linear dimensions of the forehead region and inion. In our sample, we observed a more spheric neurocranium in females, as females had a more vertical and dome-shaped forehead, a less prominent glabella and inion region, and a relatively lower cranium in the region of the bregma. Franklin et al. (2006a) reached similar conclusions with a series of South African crania, just as Šmahel et al. (1998) did with a Czech population.

Conclusion

Our results show that a higher success rate in classifying the shape of crania according to sex may be attained by analysing individual regions of the cranium, rather than by including models that characterize the cranium as a whole, with all its landmarks, in the analysis. The success rate of sex differentiation is also higher than when using routine discriminant function analysis of linear dimensions. These findings are in line with the requisites of practice and the state of preservation of the available material. GM is a suitable tool for determining sex, and such research deserves increased attention. Determining whether sexual dimorphism of cranium shape shows logical homology in various populations will be made possible by comparing the results of classification among groups of crania from various geographically or chronologically distant populations.

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Surface facial modelling and allometry in relation to sexual dimorphism

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ABSTRACT

Sexual dimorphism is responsible for a substantial part of human facial variability, the study of which is essential for many scientific fields ranging from evolution to special biomedical topics. Our aim was to analyse the relationship between size variability and shape facial variability of sexual traits in the young adult Central European population and to construct average surface models of adult males and females. The method of geometric morphometrics allowed not only the identification of dimorphic traits, but also the evaluation of static allometry and the visualisation of sexual facial differences.

Facial variability in the studied sample was characterised by a strong relationship between facial size and shape of sexual dimorphic traits. Large size of face was associated with facial elongation and vice versa. Regarding shape sexual dimorphic traits, a wide, vaulted and high forehead in combination with a narrow and gracile lower face were typical for females. Variability in shape dimorphic traits was smaller in females compared to males. For female classification, shape sexual dimorphic traits are more important, while for males the stronger association is with face size.

Males generally had a closer inter-orbital distance and a deeper position of the eyes in relation to the facial plane, a larger and wider straight nose and nostrils, and more massive lower face. Using pseudo-colour maps to provide a detailed schematic representation of the geometrical differences between the sexes, we attempted to clarify the reasons underlying the development of such differences.

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Introduction

The human face provides a range of information about the given individual regarding his or her sex, age, health, emotional state of mind and membership in an ethnic group. The structure and form of the human face and the position of the eyes, nose, lips and jaws with respect to each other are mostly genetically determined (genome, proteome, and metabolism), but environmental exogenous factors also play an important role in facial variability.

Cranial components derive from embryologically distinct regions. They develop in a morphologically integrated manner (e.g. Enlow, 1968; Cheverud, 1982) through numerous morphogenetic (e.g. neural) and functional (e.g. masticatory, respiratory) interactions (Lieberman et al., 2000). The harmonious interaction of bones, mandibular and cervical joints, facial and cervical muscles, connective and fatty tissue as well as nerve tracts gives rise to the extensive variation of facial structure (Fanghänel et al., 2006).

Sexual dimorphism is a component of facial variability, which may result from natural selection (Slatkin, 1984) and other genetic, structural or behavioural constraints (Lieberman, 1995). Sexual dimorphism of the shape and form of the face is already present in the early prenatal period (Fink et al., 2005), but it does not develop fully until the period of pubertal growth (Enlow and Hans, 1996). During early foetal life, craniofacial and cerebral morphogenesis constitutes a unitary process (Hennessy et al., 2005).

The nature of sexual dimorphism changes with age. Four factors appear to contribute to cranial sexual dimorphism during human postnatal development. These are the initial, probably prenatal differences in shape, the differences in the association of size and shape, male hypermorphosis and some degree of difference in the direction of male and female growth trajectories (Bulygina et al., 2006).

An early hormonal environment of high foetal testosterone could correspond to a somewhat more robust male-like facial shape, whereas high foetal oestrogen could correspond to a more gracile female-like facial shape (Lutchmaya et al., 2004). According to Fink et al. (2005), the human face may be a composite of at least two factors operating differently on facial shape – the prenatal environment and the actual chromosomal sex. In the postnatal period, testosterone affects a number of facial features. In most age classes, a statistically significant sexual dimorphism is found in all linear, surface and volume measurements, male values being larger than female values. Exceptions have been found in the 11–12-year-old age group in concurrence with the earlier female peripubertal growth spurt (Ferrario et al., 1998).

Ursi et al. (1993) found that a number of craniofacial dimensions, such as the anterior cranial base length, are significantly larger in males from age 6 years onwards. Bulygina et al. (2006) have described a low correlation between newborn and adult morphology, while 3-year-olds already show a high correlation with their adult form. The adult pattern of inter-individual differences in facial form in a single human population is established within the first few years of life.

Enlow (1990) has suggested that girls and boys do not differ in facial characteristics until about 13 years of age, when pubertal facial growth slows down in females but continues in males. A number of other studies have shown that girls and boys do not differ in facial characteristics until about the age of 13 years (e.g. Bishara et al., 1984; Genecov et al., 1990; Farkas and Posnick, 1992). At the age of fifteen years females tend to have more prominent eyes and cheeks in relation to males. Males tend to have more prominent noses and mouths (Toma et al., 2008).

In pubertal males, a high testosterone-to-oestrogen ratio causes an overall elongation of the face, relatively smaller eyes, a larger nose, the lateral growth of the cheekbones, mandible and chin, the forward growth of the superciliary arches and glabella region and the lengthening of the lower face, giving the face a more robust shape. The influence of oestrogen leads to a more gracile and rounded shape of the face with high eyebrows, a more gracile nose and chin and fuller lips (e.g. Farkas, 1981; Enlow and Hans, 2008; Ferrario et al., 1998; Schaefer and Bookstein, 2009). The principal sexual dimorphic difference is the size and configuration of the nose and nasopharynx, which leads to collateral differences in other topographic structures of the face (Enlow and Hans, 2008). The physiologically increased requirement for air intake in males has been proposed to give rise to sex-specific morphological configuration in the craniofacial complex (Rosas and Bastir, 2002).

The size of the adult craniofacial complex is impossible to express using isometric function, but it is associated with some shape changes. The adult skull, as a highly organised morphological structure, is influenced by the presence of so-called static allometry. The contribution of size to the shape differentiation of the sexes can be studied on the basis of centroid size and its relation to sexual dimorphic traits. Centroid size (Bookstein, 1991) is defined as the square root of the sum of the squared Euclidean distances from each landmark to the mean of the configuration of landmark coordinates. It is an expression of overall size of a morphological structure.

The method of geometric morphometrics (dense correspondence model analysis and finite element scaling analysis) enables the evaluation of the whole surface area of the face and the precise identification of sexual dimorphic traits, including the possible interpretation of their development. Surface analysis provides strikingly more anatomical information compared to classical morphometrics or landmark data analysis. An important example is the possibility of analysing large areas of the face that are not recorded by landmarks, such as the cheeks, jaw, orbits and forehead (Hennessy et al., 2005). Similar to computerised 3D images, this method is fast, non-invasive and allows the analysis of soft tissue characteristics across/through the full 3D spectrum (Da Silveira et al., 2003).

Using 3D images of the faces of young adult males and females from the Central European population, we first aimed to analyse the relationship between size and shape variation of sexual traits in the face. The static allometry of the whole facial surface has not yet been studied. We verified the assumption that the contribution of size to form differences between male and female faces will be less in comparison to shape differences.

The second aim was to evaluate the differences between the average female and male face. Using finite element scaling analysis (FESA), we visualised the size and shape differences between the average female and male face on the basis of the fractional smallest facial units in the form of pseudo-colour maps. Such an approach helped to clarify the development of certain selected dimorphic traits.

Materials and methods

Three-dimensional images of the faces of a total 100 individuals from the Czech, i.e. Central European, population were used for this study. The study included 50 males with an average age of 21.1 years and 50 females with an average age of 21.6 years. These adults were students of the Faculty of Science and the Faculty of Humanities, Charles University in Prague. The sample included only probands of Czech nationality, with no facial defects. The images were scanned in the 3D laboratory of the Department of Anthropology and Human Genetics, Faculty of Science, Charles University in Prague, Czech Republic in the period between October 2007 and December 2008.

The faces were scanned using an InSpeck 3D MegaCapturor II (Creaform Inc., Québec, Canada) and InSpeck FAPS software (Creaform Inc., Québec, Canada). The InSpeck 3D digitiser is a non-contact scanner. It is capable of capturing the 3D shape of a human face within seconds and is based on white halogen light technology, which is completely safe for humans. The scanner output is a surface model of the face, including its texture (three-dimensional photograph), which has to be further edited and cleaned using the appropriate RapidForm XOS software (INUS Technology, Inc., Seoul, Korea). This procedure includes cleaning, merging of multiple scans, hole filling, decimating and smoothing (Fig. 1).

Hutton et al. (2001, 2003) have optimised the number of reference landmarks ($N=9$) that must be localised manually on each analysed facial model in order to convert the models to the same number of triangular faces using dense correspondence model analysis, i.e. including vertices or individual landmarks. One model is selected as the basic (reference) model, and the position of the whole polygon mesh of the individual models is calculated on the basis of the location of these 9 landmarks, i.e. mutually corresponding points. This calculation is based on a generalised Procrustes analysis, which helps to calculate the average position of the reference landmarks. Every surface model of all individuals is transformed using the TPS (thin-plate spline) method into an average (consensual) configuration of the nine basic landmarks. Using a closest point search, for each vertex of the base mesh the nearest vertex in the other polygonal meshes is found. All points of the basic model are thus allocated an identical number of corresponding points on the basis of the shortest distance. All points or vertices of the polygon mesh may be further considered as landmarks, and we may consider them to be the initial data for multivariate analysis (see below).

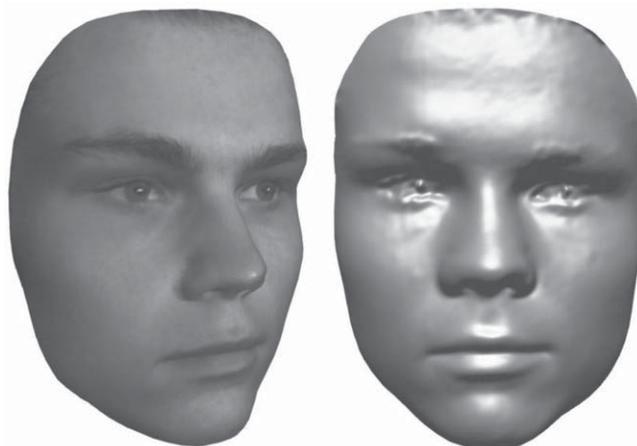


Fig. 1. Adjusted 3D model of the face. Left – texture; Right – surface model.

Principal component analysis (PCA) was used to explore the relationships between the mean male and female faces and their variability. This method was used both with and without normalising the size. In view of the studied sexual dimorphism of facial shape, we mainly focused on the components of facial variability that best express it, i.e. those components that separate male and female samples in the best possible way. Linear regression was used to describe the relation between centroid size and shape sexual traits. Discriminant function analysis with cross-validation was performed to assess the sex classification accuracy of the discriminant functions (on PC scores of the first and second component) when size is normalised and when size is preserved.

In order to demonstrate changes in area size and shape, a finite element scaling analysis (FESA) was undertaken that incorporated the spline interpolation function. Based on this approach, differences in form can be visualised graphically (Singh et al., 1999). A log-linear interpolation of the values of changes in area or shape was used to generate a pseudo-colour map, which provided a graphical demonstration of geometrical differences (Singh and Thind, 2003). The results of FESA are in the form of coloured maps coding the facial areas according to differences in size or shape. The most pronounced increase in surface area (pink colour) exceeds 100%; neutral modification (green colour) is approx. 0% and a relative decrease in surface area (dark blue colour) may, in contrast, be up to –100%. Dense correspondence model analysis, PCA and FESA were performed using MorphoStudio v3.02 software (Biomodeling Solutions LLC, Portland, Oregon, USA) and Morphome3cs (cgg.mff.cuni.cz/trac/morpho).

Results

Facial size and shape variability with respect to sexual dimorphism

First, the variability of facial shape and size in the young adult Central European sample was evaluated in order to describe the sexual dimorphism of size and shape as a whole. The results of PCA are shown in Fig. 2. Sexual dimorphism in shape and size was best characterised by components PC1 and PC2, which together were responsible for 56% of the variability. The component PC1 (x -axis) represented the most significant principal component, which was responsible for 42.8% of the variability, especially in the size of the face. The PC2 component (y -axis) described 13.1% of the variability and was above all a component of the height-width facial relationship. The scatter of males and females was not fully separated, as the faces of a small portion of the males and the females were similar to each other.

Sexual dimorphism using a hyper-masculine and hyper-feminine face is illustrated in Fig. 3A. These two shapes corresponded to the position of points HM (hyper-masculine) and HF (hyper-feminine) on

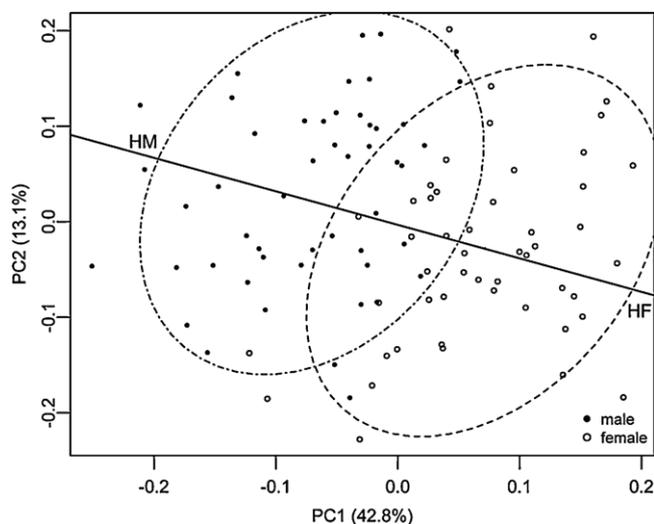


Fig. 2. Graphical result of the principal component analysis (PCA) after Procrustes transformation without scaling. Relation of the 1st and 2nd components, which explains the sexual dimorphism of the studied sample. The diagonal is the line passing through the centroids of the samples' scores and represents the inter-sexual line of morphological differences from the hyper-masculine (HM) to the hyper-feminine (HF), clearly illustrated in Fig. 3A.

the diagonal line passing through the centroids of the male and female face score clusters in Fig. 2. The transformation of a masculine face into a feminine face was associated with the following changes: The face decreased in size and at the same time relatively widened. The prominence of the eyebrow ridges decreased as they shifted laterally, with the distance between the eyes increasing simultaneously. The eye fissure was less deeply located in relation to the facial plane and widened progressively. The glabellar area flattened, and the naso-frontal junction became more continuous. The size of the nose, including the nostrils, decreased and its tip pointed more upwards. The area of the lower face differed especially in terms of the amount of soft tissue and the chin width, whereby the musculature gradually decreased and the chin narrowed and became more pointed.

The results of PCA after Procrustes transformation of the data, including size normalisation, are shown in Fig. 4. Sexual dimorphism in shape was characterised only by component PC1 (46.9% of the variability). The variability of male dimorphic traits was higher compared to female traits. It seems that after size elimination, half of the males had faces similar to those of the females.

Sexual dimorphism of the hyper-masculine and hyper-feminine shape traits is described in Fig. 3B. Concerning facial proportionality, negative PC1 (hyper-masculine) values corresponded to a narrow forehead and wide face and vice versa. These proportions were reflected in all individual parts of face. Towards the positive values of PC1 the inter-orbital distance increased, as well as the base of the nose. On the other hand, the lower face narrowed, including the nose, mouth and chin. When moving towards feminine faces, the height of the forehead increased simultaneously with decreasing facial height. The position of the forehead with respect to the facial plane changed from sloping to perpendicular and vaulted. A slightly convex masculine nose changed into a finer, slightly concave feminine nose.

As mentioned above, sexual dimorphism was related to size. However, the sexual dimorphic traits became more apparent when size was eliminated (see Fig. 3A and B). Fig. 5 documents the relationship between centroid size and PC1, which was significant ($R = -0.48$; $R^2 = 0.23$; $p = 3.8892 \times 10^{-7}$). These findings show that sexual dimorphism represented by PC1 strongly correlates with centroid size. Discriminant analysis with cross-validation yielded 90% accuracy in sex determination using PC scores, including size (Hotelling $T^2 = 139.71$; $n = 98$, $k = 2$; $F = 69.14$; $p = 2.16 \times 10^{-19}$). When the size was normalised, the accuracy was reduced to 73.27% (Hotelling $T^2 = 55.44$; $n = 98$, $k = 2$, $F = 27.44$; $p = 3.4 \times 10^{-10}$). In other words, size was a substantial part of the sexual dimorphism in our sample.

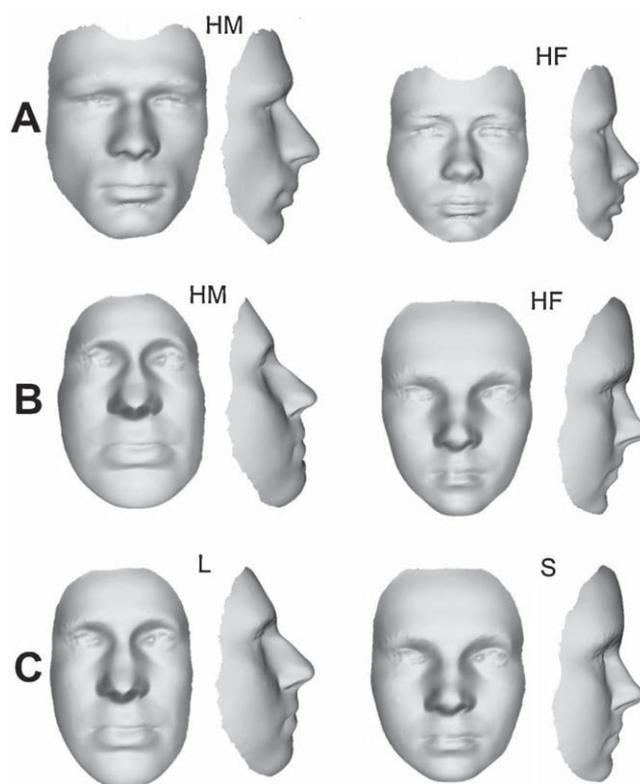


Fig. 3. Facial sexual dimorphism in the studied sample. (A), Inter-sexual differences in shape and size from the hyper-masculine (HM) to the hyper-feminine (HF) face, which correspond to the marked positions on the diagonal in the graph in Fig. 2; (B), Inter-sexual differences in shape after size normalisation from the hyper-masculine (HM) to the hyper-feminine (HF) face, which correspond to the marked positions on the diagonal in the graph in Fig. 4; (C), Allometric shape changes in relation to large (L) and small (S) faces. Left – norma frontalis, Right – norma lateralis.

Shape changes related to centroid size are illustrated in Fig. 3C. The basic relation was that large faces were elongated, while small faces were more rounded. In detail, large faces were connected with a low and flat forehead, a closer inter-orbital distance, a convex shape of the nose, and a wider mouth and chin. Conversely, for a small face, a higher and vaulted forehead, a wider inter-orbital distance, a concave shape of the nose, and a thin mouth and chin were typical. In other words, large faces corresponded with more masculine traits and vice versa.

Sexual dimorphism evaluated using finite element scaling analysis (FESA)

FESA was used to evaluate the differences between the average female and male face. The differences between the average faces were divided into size differences (Fig. 6) of particular facial surfaces (triangular faces) as well as into shape differences (Fig. 7). In both cases, size and shape deformation, the average female face was used as the initial (reference) object and transformed into the average male face. The pink and red to orange shades represent areas larger on average in males; green denotes the absence of sexual dimorphism, and the shades of blue denote areas that were larger in females.

It was apparent that size differences (Fig. 6) between female and male faces existed in both directions, although the larger size of segments of the male face dominated markedly. A visible positive difference (i.e. in favour of males) was clear in the area of the nose (or rather the contours of the nostrils), the mouth and the lateral marginal areas of the face. These areas were larger in males by 60–85%

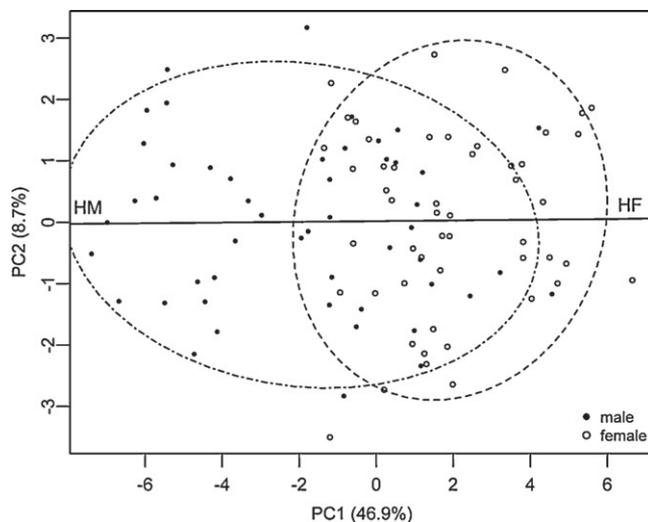


Fig. 4. Graphical result of the PCA after Procrustes transformation including scaling. Relation of the 1st and 2nd components, where the PC1 explains the sexual dimorphism of the studied sample. The line passes through the centroids of the samples' scores and represents the inter-sexual line of morphological differences from the hyper-masculine (HM) to the hyper-feminine (HF), clearly illustrated in Fig. 3B.

on average, whereby, e.g. the contours of the nostrils showed up to an ~85% difference compared to females. A relatively large positive difference was seen especially in the corner of the eye and eyebrow ridges, where certain sections demonstrated up to a ~59% difference. The nasal region and the contour of the upper lip demonstrated an apparent positive difference ranging from 25% to 59%. Differences of 15–24% in size occurred in the area of the eyebrow ridges, the lateral margins of the forehead, the nostril wings, the masseter muscle region and, surprisingly, in the glabellar area. Smaller differences in favour of males were again clear in the area of the glabella, which demonstrated in certain sections

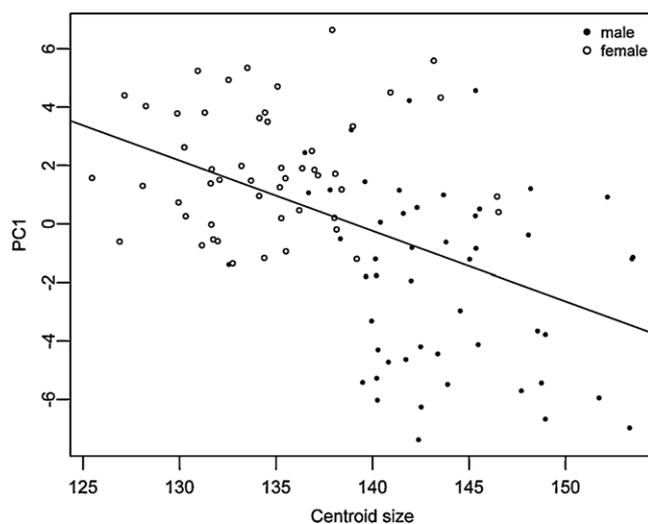


Fig. 5. Relation between shape sexual dimorphism and centroid size analysed using a linear regression model. $R = -0.48$; $R^2 = 0.23$; $p = 3.8892 \times 10^{-7}$.

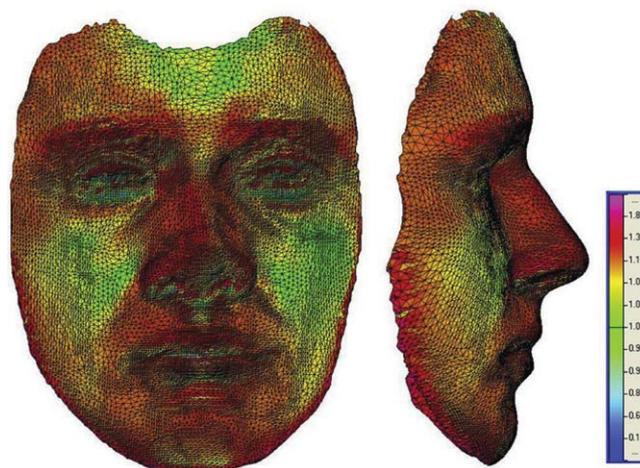


Fig. 6. The resultant diagram of finite element scaling analysis (FESA). Differences in size between average female (reference) and male faces. The colour coding (shade difference on black-and-white photograph) of individual surface elements characterises the difference in the size of the given segments (pink and red colours [darker shade on a black and white photo] illustrate larger segments in males, blue colour [lightest shade on a black-and-white photo] corresponds to larger segments in females, green colour [intermediate-to-light shade on a black-and-white photo] indicates segments without size differences).

a mere 6% difference. Most of the forehead, cheeks and lower chin were larger as well, with a 20% difference. No or minimal difference was apparent in the central section of the cheeks and in most of the forehead.

As to differences in shape (Fig. 7), it may be said that on average there were fewer common deformation differences between females and males compared to size differences. The greatest differences in shape in favour of males were recorded in the area of the medial margin of the orbit, the area of the nostrils, the mouth and certain parts of the marginal facial contours (40–80% difference). The marginal sections of the face, the internal upper margin of the orbit and the area below the nose demonstrated

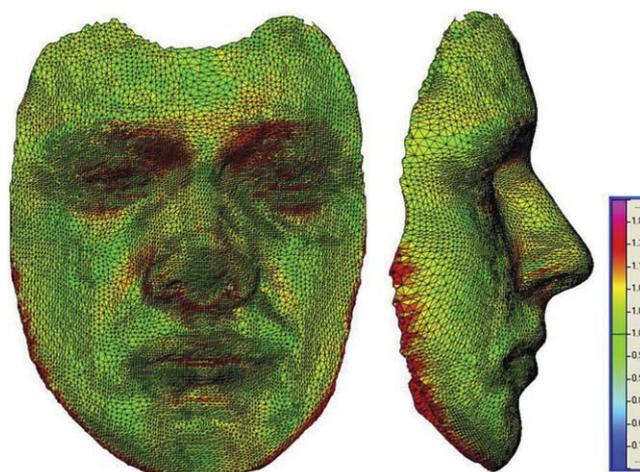


Fig. 7. The resultant diagram of finite element scaling analysis (FESA). Differences in shape (deformation) between female (reference) and male faces. The colour coding (shade difference on a black-and-white photograph) of individual surface elements characterises the difference in the shape of the given segments (pink and red colours [darker shade] illustrate shape differences in segments in favour of males, green colour [lighter shade] corresponds to segments without shape differences).

a 20–39% difference. Minimal positive shape differences (i.e. in favour of males) of 5–9% occurred, e.g. in the mid-section of the forehead, in the small triangular areas below the eyes and in the area of the line moving laterally downwards from the nostril wings.

Discussion

Sexual dimorphism of facial size

Sexual dimorphism of facial size is a consequence of the fact that the course of craniofacial growth differs significantly between male and female faces during ontogenetic development. The dimensions of adult male faces are larger compared to those of females, a finding that has been described many times in multiple reports (e.g. Borovanský, 1936; Ferrario et al., 1993, 1998; Budai et al., 2003; Božič et al., 2009). Some sexual differences in facial dimensions are larger, others are smaller, because growth is not an isometric process. Ferrario et al. (1993) and Šmahel et al. (1998) stated that the inter-sexual differences in the size of most linear facial characteristics in adults reach 5–10% of overall trait size. According to many studies, in adulthood, inter-sexual facial differences are more significant in terms of size than in terms of shape (e.g. Ferrario et al., 1998, 2000).

Facial soft-tissue thicknesses vary with craniofacial size. Males had thicker soft tissues and larger craniometric dimensions than females (except in the region of the cheeks) but sex differences were very small. Considerable overlap of ranges was also noted. It was found that the variation within each sex was large while the variation between the sexes was small (e.g. Simpson and Henneberg, 2002; Stephan et al., 2005; Stephan and Simpson, 2008).

It is difficult to infer shape differences from linear measurements. Concerning facial angles and indices, they do not provide complete information about the facial shape and its variability, as some of them are sexually dimorphic and others of them are not (Halazonetis, 2007). Such a mutual connection between size and shape characterises allometry, which used to be studied on the basis of geometric morphometrics.

In our study, when the size factor is not excluded from PCA analysis, the most significant proportion of variability was associated with face size (PC1 43.9%). Larger faces usually correspond to males, but it was not possible to distinguish which sexual traits were related to size and which not. Similar to other authors (Rosas and Bastir, 2002; Kimmerle et al., 2008; Schaefer and Bookstein, 2009; Gonzalez et al., 2011; Weisensee and Jantz, 2011), we analysed static allometry using centroid size and its relation to sexual dimorphism in the next step of our study. Using a linear regression model, a significant correlation between centroid size and sexual dimorphism was confirmed. Static allometry demonstrated that large faces were elongated, while small faces were more rounded.

The results of linear regression showed that small faces are connected with feminine dimorphic traits, while males more often have larger faces. It seems that for female classification, shape sexual dimorphic traits are more important, while for males the stronger association is with centroid size.

Rosas and Bastir (2002) and Kimmerle et al. (2008) also studied the relation between static allometry, shape and sexual dimorphism, but in a somewhat different situation. They analysed not only the face but also the skull as a whole, and not all of the surface but only a group of landmarks. According to the results of Rosas and Bastir (2002), the mean male centroid size was significantly larger than the mean of the female subset. The influence of centroid size on shape (allometry) revealed a shift in the proportions of the neurocranium and the viscerocranium, with a marked allometric variation of the lower face. Both size and sex had significant influences on shape. Similarly, in our study, with decreasing centroid size, the forehead became larger and the mandible region more gracile. In addition, we found that centroid size was connected with other sexual dimorphic traits such as inter-orbital distance and the shape of the nose. In contrast to our results, Kimmerle et al. (2008) found that size does not have a significant influence on shape; in their sample, smaller and larger individuals within the same sex were similar in shape.

Weisensee and Jantz (2011) described a static allometric model with sexual dimorphic traits. In females, the zygomatic arch becomes wider (in agreement with our results) and the cranial base is more superiorly positioned, while in males there is an increase in facial height (in agreement with our results). Similar to our study, according to Hennessy et al. (2002) and Evison et al. (2010),

sexual dimorphism is evident in both size and shape and shows patterns that affect male and female individuals differently.

Sexual dimorphism of the upper third of the face

The aim of our study was to clarify certain individual features of sexual dimorphic traits as part of inter-individual variability. According to Spiegel (2011) the upper third of the face is the most significant part of the face for determining the female sex in both frontal and profile views. In this paper we studied the neuro-cranial region only in the area of the forehead, where the more sloping forehead in males was associated with prominent eyebrow ridges and glabella. Such a result was similar to that reported in another geometric morphometric (GM) study on a Prague sample from the first half of the 20th century (Bigoni et al., 2010), a GM study on a southern African sample (Franklin et al., 2006a) as well as a more recent study (Hennessy et al., 2005). Glabellar prominence is usually associated with the muscles of facial expression (Schiwy-Bochat, 2001; Çelbiş et al., 2001) and the size of the masticatory apparatus, which affects the robustness of the facial skeleton overall (Franklin et al., 2006a). According to Enlow and Hans (2008), this sexual trait is associated with the size of the frontal sinus. The inner and outer tables of the superorbital part of the forehead diverge, and the cancellous bone between them develops into the frontal sinus. Because the nasal part of the male face continues to grow for several years beyond the growth period typical for the female face, the male frontal sinus is much larger.

In association with the masculine shape of the forehead in our sample, the eyes were located deeper in relation to the facial plane, with the superomedial area of the orbit demonstrating stronger inter-sexual differences than the area of the eyebrow ridges or nasal ridge. Likewise, other GM studies have demonstrated rather large sexual differences in the orbital region (Hennessy et al., 2002; Pretorius et al., 2006; Mendelson et al., 2007; Nagasao et al., 2007; Bigoni et al., 2010). We propose that sinus enlargement in conjunction with size differences in certain areas of the orbit might cause the difference in the prominence of the glabella and eyebrow ridges. These results are in concordance with those, for example, of Hennessy et al. (2002), Hennessy et al. (2005) and Toma et al. (2008) for fifteen-year-old individuals.

From the evolutionary point of view, orbital convergence in humans is about 80°, causing about 140° of the visual field to be binocular. Greater orbital convergence in the human leads to a much larger degree of binocular overlap and more stereoscopic perception (Bruce et al., 1996; Lieberman, 2011). The distance between the eyes was on average shorter in the males of our sample. The orbits of males were more or less parallel to the frontal plane, whereas those of females were oriented more in the sagittal direction (Bigoni et al., 2010). In our opinion, these results, in association with those of Lieberman (2011), indicate that males have on average better binocular vision than females. This finding could be associated with different sex roles during evolution.

Sexual dimorphism of the middle and lower third of the face

According to our results on the mid-facial region, it is apparent that males have a more convex profile and a wide straight or convex nose with a deeper naso-frontal transition area that is not continuous (in agreement with Enlow and Hans, 1996; Bigoni et al., 2010).

Males present with a relatively larger size of the nose and larger and more flaring nostrils. The intra-membranous bones of the middle and lower portions of the face grow around the oropharynx and nasopharynx and are induced to a large extent by airflow resistance (e.g. Cooper, 1989; Warren et al., 1987). It was demonstrated that the male nasal cavity increases anteriorly (piriform aperture) and posteriorly (choanae) (Franklin et al., 2006a; Bigoni et al., 2010). In view of this fact, it was hypothesised that sexual differences could be associated with body composition and energy requirements. When breathing through the nose, the augmented nasal cavity responds to physiological needs. Our data document that the nose region is indeed larger in males, which is in concordance with the results reported by many authors (e.g. Ferrario et al., 1993; Baik et al., 2007; Božič et al., 2009). According to the hypothesis of Rosas and Bastir (2002) and Enlow and Hans (2008), the size of the nose and the soft tissue of the nostrils could also be important for oxygen requirements. The female nose is

narrower, reduced in area and displaced posteriorly; the tip of the nose is located more posteriorly so the nose becomes relatively shorter than in males (Hennessy et al., 2005), which is in agreement with our results.

In our study the male face was relatively narrower with slightly prominent cheeks, a smaller amount of soft (probably fatty) tissue in the cheeks and, in contrast, a massive musculature surrounding the mouth and converging into a wide and slightly prominent chin. These results are also in concordance with those of Hennessy et al. (2002, 2005), who analysed the surface of the human face using geometric morphometrics. Female cheeks expand in area and are displaced outwards. Their chin is reduced in area and is displaced superiorly and posteriorly; the mandible is reduced in relative length. In other words, significant differences in shape are demonstrated by the lower third of the face, which in males is usually larger and displaced more forward and downward (in agreement with Ferrario et al., 1999; Franklin et al., 2006b).

Mechanical strain due to masticatory force influences lower and mid-facial growth along a complex strain gradient, with more dominant effects occurring in the mandible and zygomatic arches and less significant effects occurring further away from the teeth or muscle attachment sites (e.g. Carlson and Van Gerven, 1977; Kiliaridis et al., 1986). In the lip evaluation studies of Ferrario et al. (2000) and Sawyer et al. (2009), a statistically significant sexual dimorphism was found in all linear, surface and volume measurements, with male values greater than female values, which is in agreement with our results. The upper lip and philtrum are displaced posteriorly and superiorly in females (Hennessy et al., 2005).

Dense correspondence model analysis and PCA methods proved their worth in the study of the 3D variability of facial morphology. They enabled size and shape separation and therefore the detailed evaluation of sexual dimorphic traits. The differences may be evaluated in the right-left, superoinferior and anteroposterior directions. Methods used here enable the acquisition of average surface models of adult males and females and the comparison of the shape of fractional facial units between normal and pathological states or between samples of developing patients in the future.

Conclusions

1. Static allometry is a substantial part of sexual dimorphism. Large size is related to facial elongation, while small faces are more rounded.
2. The sexual dimorphism of the shape is expressed by the width proportionality of the face. Masculine faces display a low and narrow forehead in combination with a wide lower face. For feminine faces, a high, vaulted and wide forehead is associated with a narrow and less prominent lower face. For female classification, shape sexual dimorphic traits appear to be more important, while for males, there is a stronger association with size.
3. The forehead in males is more sloping, while the eyes are closer to each other and located deeper in relation to the periorbital area. The position of the eyes shows stronger inter-sexual differences than the area of the glabella, the eyebrow ridges or the nasal ridge. The deeper position of the eyes in males, in combination with a narrower eye fissure, is probably the consequence of a larger and more protuberant frontal sinus in males.
4. In the mid-facial area, the male external nose is enlarged anteriorly (a larger and convex nose) and the nostrils are strikingly larger and more flaring. The face is relatively narrower with less prominent cheeks and a smaller amount of soft (probably fatty) tissue in the cheeks.
5. The lower face in males is wider laterally with massive, well-shaped musculature enveloping the mouth aperture. Another typical male trait is a wide and prominent chin.

Acknowledgements

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Příloha F

Skull Shape Asymmetry and the Socioeconomic Structure of Early Medieval Central European Society

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ABSTRACT The socioeconomic structure of the Early Medieval society from Mikulčice settlement (Czech Republic) was studied on the basis of an evaluation of the fluctuating and directional asymmetry of skulls. Two distinct inhabited regions, castle and sub-castle, were compared. Fluctuating asymmetry is used as a bioindicator of environmental stress, which is thought to have been different in the Mikulčice castle and sub-castle regions. Directional asymmetry indicates biomechanical loading, and it was expected that it would reflect different subsistence patterns. The material consisted of 129 crania from what are assumed to be a higher socioeconomic class (Mikulčice castle) and 71 crania from the middle and lower socioeconomic classes (Mikulčice sub-castle). As a comparative sample, 138 crania from the lowest socioeconomic groups (Pachner Collection) were used. The three-dimensional coordinates of 68 landmarks were digitized and analyzed using geometric morphometrics. In terms of directional asymmetry, the highest values were recorded in the sub-castle sample and confirmed their lower socioeconomic position, with a grittier and low-protein diet, as compared to castle. The lowest directional asymmetry values were found in the Pachner Collection, with an assumed more liquid diet. In terms of fluctuating asymmetry, distinctive differences between the sexes were found. In males, no differences were depicted between castle and sub-castle, and the lowest fluctuating asymmetry values were recorded. In females, significantly higher values of fluctuating asymmetry were found surprisingly in castle, conformable to the most stressed Pachner Collection. We expect that fluctuating asymmetry reflects the more variable castle females, in consequence of patrilocality.

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At the beginning of the 9th century A.D., the western branch of the Slavs managed to establish a state in Central Europe, the so-called Great Moravia. This first Slavic state (Poulik, 1975; Havlík, 1978) dated to the 9th -10th centuries A.D., stood politically and culturally on the frontier of Byzantium, Rome, and the Frankish empire (Poláček, 2008). According to

written, archeological, and anthropological sources (Stloukal and Vyhnánek, 1976; Havlík, 1978; Poulík, 1985; Velemínský and Poláček, 2008) Great Moravia represents a society with complex social stratification. One of the most important centers of Great Moravia was the Mikulčice settlement. Mikulčice played the role of an important communication crossroads (Květ, 1999), and simultaneously provided favorable living conditions for its local inhabitants (Poláček, 2008). Since the first field researches in the 1950s (Poulík, 1975, 1985; Klanica, 1985) distinct inhabited regions have been discovered in the Mikulčice settlement: a fortified acropolis (castle), partially fortified sub-castle, and rural hinterland (Poláček, 2008). Archeologists have described social differences between the residential center, with a number of churches, burial grounds, and a handicraft industry, and its rural hinterland. A question remains as to how distinctive were the socioeconomic differences between castle and sub-castle (Poláček, 2008; Macháček, 2010).

The Mikulčice settlement was located in the valley of the Morava River. The center on the sand dunes enjoyed the natural protection of river channels (see Fig. 1). The castle region, with the princely residence and a number of churches, represented the main residential and spiritual area of the agglomeration (Poláček, 2008). Several burial grounds were excavated close to the central churches, inside the first fortification. The central burial grounds are considered to represent the highest social class of society, as the church and especially relics have been noted to have played a principal role in the Early Middle Ages (Ohler, 2001; Buko, 2008). Evidently this separation is not strict, because in the castle locale there could also be buried people who were directly connected with the princely palace, such as craftsmen or inhabitants providing services for the residence (Poláček, 2008).

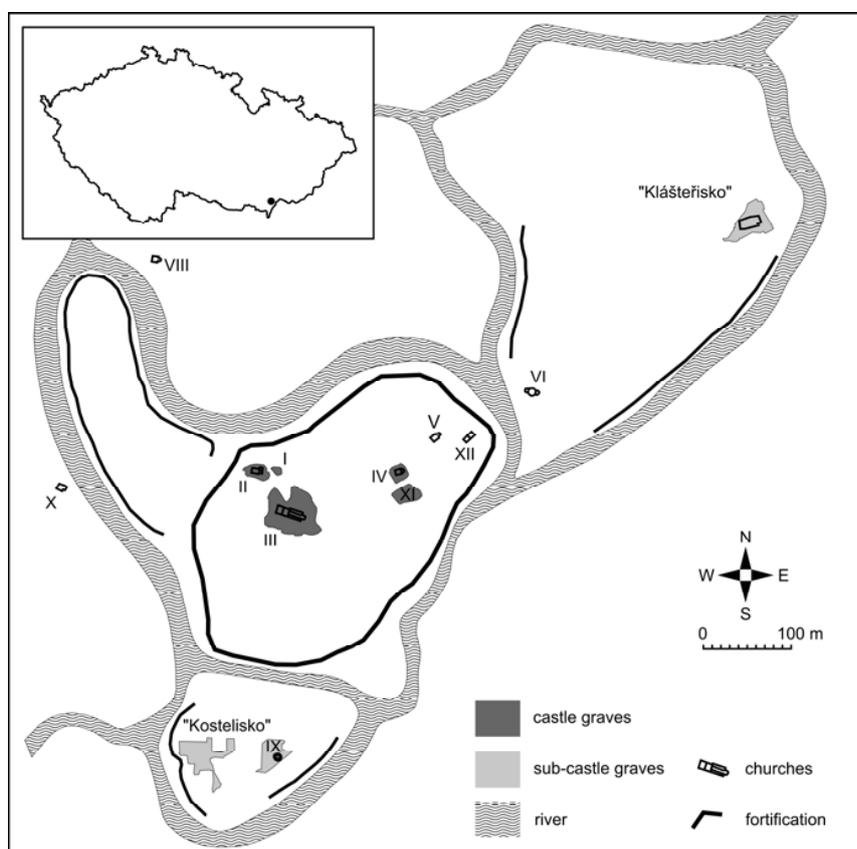


Figure 1. The map of Mikulčice settlement.

Outside of the fortification, other burial-grounds existed in the sub-castle region. It is assumed that representatives of the middle and lower socioeconomic classes were buried here, in the burial sites, e.g., Kostelisko, around the IXth church, and Klášteřisko (Stloukal and Vyhnánek, 1976; Havlík, 1978; Poláček, 2000, 2008). The churches in the sub-castle are thought to have been parts of the estate founded by nobles in the vicinity of the princely residence, which is also a possible explanation for the finds of rich warrior graves, especially in

the Kostelisko area (Poláček, 2008). The sub-castle inhabitants evidently participated in ensuring the running of the center and in providing services for the privileged classes, include the military personnel (Klanica, 1987; Staňa, 1997; Poláček and Marek, 2005; Hladík et al., 2008).

The identification of socioeconomic differences in Mikulčice presents several difficulties. The Mikulčice settlement cannot be unequivocally identified as one of the locations cited in contemporary written sources (Poláček, 2008). Written records, such as codes of law, chronicles, patrimonial letters, or military reports, imply significant proprietary and social differentiation in Moravian society (Havlík, 1978, 1993). Archeological findings of grave goods, a possible indicator of the socioeconomic structure of the Mikulčice settlement, could be biased by Christian ritual. On the other hand, Christianity was first adopted by the ruling layer (e.g., Třeštík, 2001; Poláček, 2008). The spread of Christianity in the lower social classes was not so rapid (Ohler, 2001; Smetánka, 2004); the influence of Christian ritual on funeral practices could only be found among all social classes as late as in the second half of the 9th century (Třeštík, 2001; Poláček, 2008). It is not distinctly known how other indicators, such as burial location or grave construction, could differentiate the social class of an individual (Stloukal and Vyhnánek, 1976; Poláček, 2000, 2008).

The study of human skeletal remains could offer another possibility for distinguishing between different socioeconomic groups (Larsen, 1999; Sládek et al., 2006). Similar to the case of written records and archeological research, this biological source also fails to yield a definite resolution regarding the Mikulčice population. No significant differences were found between the castle and other regions when analyzing stature (Dobisíková et al., 2008) or linear enamel hypoplasia related to a generalized growth disturbance (Trefný and Velemínský, 2008). Significant differences between the expected higher and lower classes were noted when analyzing the incidence of caries (Stránská et al., 2008), prevalence of enthesopathies (Havelková et al., 2011), and stable C, N isotopes from bone collagen (Smrčka et al., 2008). These studies indicate higher biomechanical stress in the lower social classes, and the much-favored millet and a greater volume of meat in the diet of the higher class. Exceptions to this conclusion were the females from the castle, who were more affected by enthesal changes than expected (Havelková et al., 2011).

We attempt to answer the question of the socioeconomic differences between castle and sub-castle by using a geometric morphometric estimation of craniofacial asymmetry. Our interest was in fluctuating and directional asymmetry, as it reflects the socioeconomic structure of the population (Palmer and Strobeck, 1986; Schaefer and Bookstein, 2009). Fluctuating asymmetry (FA) is connected with environmental stress during development and various genetic effects, such as inbreeding (Woolf and Markow, 2003; Schaefer et al., 2006; Özener and Fink, 2010). Therefore FA is used as a measure of the developmental stability, health, living conditions, and variability of a population (Doyle and Johnston, 1977; Perzigian, 1977; Palmer, 1994; Kimmerle and Jantz, 2001; Koehler et al., 2004; Willmore et al., 2005; Klingenberg et al., 2010). Some studies have discussed the presumed increased buffering the disruption of precise development in females relative to males (Klein, 2004; Møller et al., 2009), especially in samples under stressful conditions (Özener, 2010). Higher levels of FA could also be associated with rapid morphological change within a population (Kimmerle and Jantz, 2002). Craniofacial FA obtains different values in different morphological regions (DeLeon, 2007; DeLeon and Richtsmeier, 2009). Geometric morphometric craniofacial FA assessment has already been used in estimating different levels of environmental stress in humans, e.g., between people with higher and lower socioeconomic status in Turkey (Özener, 2010), between individuals from the Early and Late Christian cemetery in Sudanese Nubia; (DeLeon, 2007), and between inbred and outbred samples from an Adriatic population (Schaefer et al., 2006).

Directional asymmetry (DA) reflects biomechanical loading, which is connected with repeatable actions and human behavior. Craniofacial DA is related to masticatory function, which is associated with subsistence adaptation and associated behavior (Carlson and Van Gerven, 1977; Ferrario et al., 1997; Moreira et al., 2008; Gomes et al., 2011). Chewing habit is connected with diet, and the diet of a past population can be used to make inferences about its social stratification (Le Huray and Schutkowski, 2005). The cranial vault ossifies following asymmetric brain growth, which is dependent upon diet (Menegaz et al., 2010; Cray Jr. et al., 2011). Vault asymmetry also occurs in the context of habitual behavior, such as babies' sleeping position, cradling, or absence of unrestricted motility (Manning and Chamberlain, 1991; Turk et al., 1996; Manning et al., 1997; Cavalier and Picaud, 2008). Cranial base ossifies differently than the face and vault, as its enchondral ossification begins early in fetal life (Enlow, 1990). As shown by earlier studies, the cranial base is consistent in DA (Kwon et al., 2006).

The goal of the paper is to compare the DA and FA of the early medieval crania found in Mikulčice castle and sub-castle, in order to evaluate socioeconomic differences, using a low socioeconomic comparative sample. We expect to find that the Mikulčice sub-castle is intermediate in terms of FA, between Mikulčice castle, from higher socioeconomic groups, and the comparative sample from the lowest groups, since the sub-castle population, according to archaeological finds, represented middle and lower socioeconomic groups. In comparing DA, we expect a different picture. Since Mikulčice persisted on a hard subsistence diet, and for the comparative sample no-hard diet is proposed, we expect that both the castle and sub-castle in Mikulčice will exhibit higher levels of DA than the comparative sample. The highest level of DA will be more visible between the compared groups on the upper facial skeleton than on the vault and cranial base.

MATERIAL AND METHODS

Cranial samples

A sample of 200 adult individuals with estimated sex (Stloukal and Vyhnánek, 1976; Stloukal, 1989; Velemínský et al., 2005) was selected from Mikulčice castle and Mikulčice sub-castle (Table 1). The collection of the Mikulčice population is housed in the Department of Anthropology, National Museum in Prague. The Mikulčice castle sample, from burial grounds around the Ist, IInd, IIIrd, IVth, and XIth churches, included a total of 129 crania (61 females and 68 males). The Mikulčice sub-castle sample, from the Kostelisko and Klášteřisko burial sites, and around the IXth church, consisted of 71 crania (38 females and 33 males).

As a comparative sample, we used 138 adult crania with known sex (65 females, 73 males) from the Pachner Collection, housed in the Department of Anthropology and Human Genetics, Faculty of Science, Charles University in Prague. This identified collection originates in the 1930s and consists of poor people from Prague (Czech Republic) (Borovanský, 1936; Pachner, 1937). These people were subject to high environmental stress (Pachner, 1937), which is in agreement with other findings about this sample, such as skeletal asymmetry (Kujanová et al., 2008), low sexual dimorphism (Borovanský, 1936; Pachner, 1937), gracility of skeletons (Bigoni et al., 2005), and teeth loss (Stránská et al., 2005).

Basic descriptive statistics for some linear dimensions of the crania from Mikulčice castle, Mikulčice sub-castle, and the Pachner Collection are presented in Table 1.

TABLE 1a. Basic statistics of craniofacial linear distances in females

	MIKca F (1)		MIKsc F (2)		PACH F (3)		significant differences
	N	Mean ± SD (mm)	N	Mean ± SD (mm)	N	Mean ± SD (mm)	
Nasion-Lambda	61	171.7 ± 6.1	38	168.8 ± 4.4	64	164.6 ± 5.5	1-3***; 2-3*
Euryon-Euryon	57	138.4 ± 5.1	38	136.2 ± 5.1	64	143.3 ± 5.8	1-3**; 2-3*** 1-3***; 2-3***
Bregma-Basion	56	130.1 ± 4.9	36	128.9 ± 5.4	64	123.3 ± 4.6	3***
Prosthion-Nasion	53	66.7 ± 4.8	31	64.8 ± 3.5	49	61.7 ± 5.1	1-3***
Zygomax-Zygomax	56	91.8 ± 4.8	33	90.2 ± 4.2	64	87.1 ± 5.0	1-3***
Prosthion-Opisthion	47	126.9 ± 6.4	28	126.4 ± 5.1	49	121.1 ± 7.2	1-3*
Nasion-Basion	56	97.0 ± 4.5	36	96.1 ± 4.1	64	93.4 ± 3.7	1-3**
Mastoid-Mastoid	41	102.7 ± 4.8	27	100.4 ± 4.8	64	99.3 ± 4.7	

TABLE 1b. Basic statistics of craniofacial linear distances in males

	MIKca M (4)		MIKsc M (5)		PACH M (6)		significant differences
	N	Mean ± SD (mm)	N	Mean ± SD (mm)	N	Mean ± SD (mm)	
Nasion-Lambda	68	176.7 ± 6.1	33	174.4 ± 5.7	73	172.3 ± 6.3	4-6 *
Euryon-Euryon	67	142.3 ± 5.5	32	139.8 ± 4.6	73	147.1 ± 6.5	4-6**; 5-6*** 4-6***; 5-6***
Bregma-Basion	66	135.1 ± 4.9	32	136.7 ± 4.5	73	130.1 ± 5.8	6***
Prosthion-Nasion	59	70.1 ± 4.1	25	67.2 ± 5.7	57	66.8 ± 4.7	
Zygomax-Zygomax	65	94.2 ± 3.4	26	95.6 ± 4.9	71	90.1 ± 5.7	4-6**; 5-6***
Prosthion-Opisthion	57	133.3 ± 5.6	23	134.0 ± 6.9	57	126.9 ± 7.7	4-6**; 5-6***
Nasion-Basion	66	102.4 ± 4.7	32	102.5 ± 4.3	73	99.0 ± 4.7	4-6*; 5-6**
Mastoid-Mastoid	52	107.0 ± 4.0	23	105.8 ± 4.0	73	105.7 ± 5.1	

1MIKca, Mikulčice castle; MIKsc, Mikulčice sub-castle; PACH, Pachner's collection; F, female; M, male; number in parentheses indicates subgroups.

* P < 0.05; ** P < 0.01; *** P < 0.001.

Data acquisition

For craniofacial asymmetry assessment, 68 ectocranial anatomic landmarks (10 unpaired and 29 paired) were chosen (Martin and Saller, 1957), to provide a high level of anatomic detail of the cranium in which the landmarks were as well distributed as possible (Fig. 2; for detail, see (Bigoni et al., 2010)). On the basis of the different expected level of directional and fluctuating asymmetry in different parts of the cranium, landmarks were divided into three regions for study – upper face (29 landmarks), vault region (24 landmarks) and cranial base (23 landmarks). No landmarks around the alveolar processes were used for analysis, because of the frequent intravital loss of teeth in the Pachner Collection. All landmarks were recorded as 3D coordinates, using the MicroScribe G2X contact digitizer (Immersion Corp., San Jose, CA, USA). Each cranium, fixed in plasticine, was digitized in two positions (DeLeon, 2007). The first position on the cranial base enabled the recording of almost all landmarks chosen in the region of the face and vault. The remaining landmarks, especially on the cranial base, were then acquired in the position on the vault. In both positions, three reference points (bregma (B), nasion (N), lambda (L)) were marked on each cranium as the origin and x- or y-axis directions. These points were used to align all of the landmarks of each cranium within a common coordinate system. The combination of the superior and inferior aspects provided a complete configuration.

Skull Shape Asymmetry of Early Medieval Society

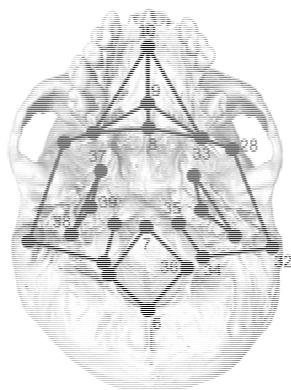
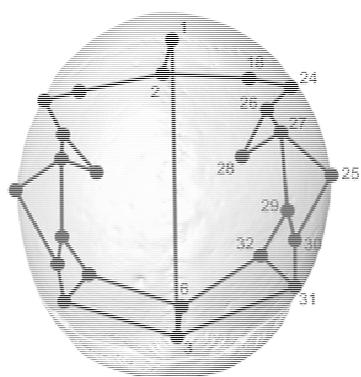
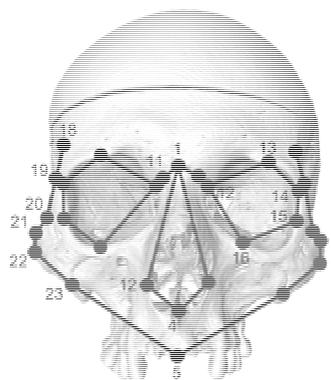


Figure 2. The location of landmarks on the upper face, vault and cranial base. For better illustration, the landmarks are linked with links similarly as in the Figure 2, 3, 4. 1, bregma; 2, nasion; 3, lambda; 4, nasospinale; 5, prosthion; 6, opisthion; 7, basion; 8, staphylion; 9, staurion; 10, foramen incisivum; 11, maxillonasofrontale; 12, maxillofrontale; 13, supraconchion; 14, frontomolare orbitale; 15, ectoconchion; 16, subconchion; 17, apertion; 18, frontotemporale; 19, frontomolare temporale; 20, jugale; 21, zygotemporale superior; 22, zygotemporale inferior; 23, zygomaxillare; 24, coronale; 25, euryon; 26, sphenion; 27, crotaphion; 28, infratemporale; 29, auriculare; 30, entomion; 31, asterion; 32, mastoidale; 33, postalverion; 34, occipitocondyilion posterior; 35, occipitocondyilion anterior; 36, foraminolaterale; 37, ovale mediale; 38, basostyloidion anterior; and 39, caroticum mediale.

Shape asymmetry analysis

For the shape asymmetry analysis of the cranium, we captured individual asymmetry (IA) and decomposed it into a sum of fluctuating (FA) and directional asymmetry (DA) using the method of Schaefer et al. (2006). On the general level, the method is based on Bookstein's geometric morphometric approach (1991).

In the first step, we aligned the whole sample by generalized Procrustes analysis and calculated the IA. Individual shape asymmetry was computed by subtracting the reflected relabeled specimen, aligned back to the original specimen by ordinary Procrustes analysis, from the original landmark coordinates. In this way, one avoids having to define the medial axis explicitly. Directions from reflected paired landmarks to the original counterparts can be interpreted as the directions that the landmark had to move from an ideally symmetric position. If unpaired landmarks are included in the analysis, associated directions express their deviation from an ideal position on the medial axis. Additionally, the average of specimen landmarks and

re-labeled reflected images form an ideally symmetric shape that is used as a reference for visualization. The sample was aligned by generalized Procrustes analysis, removing the effect of the difference in scale. Further, IA was analyzed using linear discriminant analysis with leave-one-out cross-validation, to evaluate the separability of the sample with respect to a grouping variable (sex and population). To assess the statistical significance of the difference between such groups, we performed Hotelling's T^2 test with permutation.

In the second step, DA is computed as the average of individual asymmetries. Directional asymmetry represents the bilateral variation in a sample, where one side is consistently different from the other in conformation or size (Van Valen, 1962; Palmer and Strobeck, 1986; Palmer, 1994; Klingenberg et al., 2002). The statistical significance of the DA can be measured as a fraction of DA and FA, summarized using the Frobenius norm

$D^2(X, Y) = \|X - Y\|_F^2$ and divided by corresponding degrees of freedom (Kent and Mardia, 2001).

$$T^2 = \frac{ND^2(\bar{X}, \bar{Y})/d}{\sum_{i=1}^N D^2(IA_i, DA)/(N-1)d} \sim F_{d, (N-1)d}$$

Unfortunately, this measure has an F distribution only in the case of isotropic data. This condition is rarely fulfilled in real world situations. Therefore, we used the Procrustes ANOVA, implemented in MorphoJ, described by Klingenberg et al. (2002) that can handle non-isotropic data by employing full multivariate analysis (MANOVA).

Finally, we calculated FA as the difference between the IA and DA for each individual. Thus, FA represents small random differences between corresponding parts on the left and right sides in the sample of individuals, without direction (Van Valen, 1962; Palmer, 1994). The vectors of FA were summarized and the resulting scalar values were statistically described and tested by a standard analysis of variance (ANOVA).

Fluctuating and directional asymmetry, assessed by the mentioned methodology, reflect the same biological phenomena as distance measurement does in traditional morphometrics (Palmer and Strobeck, 1986; Schaefer et al., 2006); however, we cannot expect absolute numbers with respect to particular landmarks, since the differences expressing the deviation from symmetry depends on a selection of a landmark set, because Procrustes analysis distributes the error equally among the landmarks. This behavior does not prevent us from using FA and DA for comparison. The effect of different sizes does not play an important role, because asymmetry is considered as a property of normalized objects with respect to a sample. The methodology used also allows us to quantify the FA of the whole set of landmarks without needing to remove landmarks with statistically significant DA when evaluating FA, as recommended in Palmer and Strobeck (2003), because DA and FA are both components of the IA of complete landmark configuration (Mardia et al., 2000).

As measurement error could be a confounding factor when assessing FA (Palmer and Strobeck, 1986; Robinson et al., 2002), we have digitized all of the landmarks of six randomly selected specimens six times, with a minimum of 1 day allowed between digitization. We used Procrustes ANOVA (Klingenberg et al., 2002, 2010; Klingenberg and McIntyre, 1998) to quantify measurement error. The results of measurement error assessment are presented in Table 2 and show that the variance due to measurement error is significantly smaller with respect to the FA variance.

Table 2. Procrustes ANOVA for craniofacial shape on the basis of position of all 68 landmarks

Effect	Sums of squares	Mean square	Degrees of freedom	F
Individual	0.1245	0.000247	505	6.85***
Side	0.0034	0.000036	93	1.01
Ind x Side	0.0167	0.000036	465	27.11***
Error	0.0077	0.000001	5820	

¹Individual effect represents the variation between individuals in the symmetric component of shape.

²Side, systematic difference between the original and mirrored copy of each individual, directional asymmetry.

³Ind x Side quantifies FA, effects of Side and Ind x Side represent asymmetric component of the shape.

⁴Error, the residual variation due to measurement error, includes both symmetric and asymmetric components.

⁵Mean square was multiplied by 1000.

*** P < 0.001.

Asymmetry evaluation is performed by customized calculations, according to the description in (Mardia et al., 2000; Schaefer et al., 2006) and implemented in an Octave (version 3.4.2) environment. Furthermore, a customized application was developed for the purposes of visualization and data exploration, using OpenGL and Python (version 2.7.1). Both linear discriminant analysis and statistical tests were computed in MorphoJ (version 1.03a). Supplementary computations, tables, and plots were done in Excel 2003, PAST (version 2.10, Hammer et al., 2001) and R (version 2.13.0).

RESULTS

The descriptive characteristics of the basic craniofacial dimensions and ANOVA results are presented in Table 1a, b. In females, the largest values for linear measurements were found in Mikulčice castle, intermediate values in Mikulčice sub-castle, and the lowest values in the Pachner Collection. In males, in a half of all linear dimensions, Mikulčice castle exhibited greater values than Mikulčice sub-castle, while the lowest values were found in the Pachner Collection. In both sexes, the Mikulčice samples did not differ significantly from each other. In contrast, the Pachner Collection differed significantly from the Mikulčice samples, especially from Mikulčice castle. The expected socioeconomic differences between Mikulčice castle and sub-castle were confirmed in females, but not in males. However, the Pachner Collection confirmed its expected extremely low socioeconomic position.

The individual asymmetry (IA) comparison between samples is presented in Table 3. In both sexes, Mikulčice castle and Mikulčice sub-castle did not differ in IA, but the Pachner Collection differed significantly from the Mikulčice samples. In females, a somewhat higher degree of IA in Mikulčice sub-castle was indicated by greater differences between the Pachner Collection and Mikulčice sub-castle, compared to lower differences between the Pachner Collection and Mikulčice castle females. The Mikulčice samples exhibited greater biomechanical stress than the Pachner Collection; however, differences in biomechanical loading between the Mikulčice samples were depicted only in females.

TABLE 3. *P-values of Hotelling t-test of the individual shape asymmetry between subgroups¹*

Upper face					
	MIKsc F	PACH F		MIKsc M	PACH M
MIKca F	0.305	<0.001	MIKca M	0.279	<0.001
MIKsc F		<0.001	MIKsc M		<0.001
Vault					
	MIKsc F	PACH F		MIKsc M	PACH M
MIKca F	0.304	0.028	MIKca M	0.589	0.0342
MIKsc F		0.002	MIKsc M		0.0649
Cranial base					
	MIKsc F	PACH F		MIKsc M	PACH M
MIKca F	0.720	0.155	MIKca M	0.194	0.081
MIKsc F		0.050	MIKsc M		0.644

¹see Table 1 for abbreviations.

* P < 0.05; ** P < 0.01; *** P < 0.001.

Directional asymmetry

The shape directional asymmetry evaluation is presented in Table 4. All samples exhibited significant DA in all three morphological regions. In both sexes, Mikulčice sub-castle attained the highest values of DA in all morphological regions, especially in the upper face. Intermediate DA values, closer to Mikulčice sub-castle, were attained in Mikulčice castle, with the lowest in the Pachner Collection. Thus, the Mikulčice inhabitants, mainly from the sub-castle, had to support a greater level of biomechanical loading than the individuals from the Pachner Collection. The highest differences between samples were noted in the upper face region, with the lowest and the most irregular in the cranial base.

TABLE 4. Directional asymmetry for the craniofacial shape assessed by Procrustes ANOVA¹

Sample	N	Sums of squares	Mean square ²	Deg. of freed.	F	Summarized DA /n ³
Upper face (n = 27)						
MIKca (F)	27	0.0054	0.138	39	16.8***	27
MIKca (M)	34	0.0074	0.190	39	26.78***	30
MIKsc (F)	13	0.0030	0.077	39	12.08***	32
MIKsc (M)	10	0.0025	0.065	39	7.83***	35
PACH (F)	46	0.0023	0.059	39	4.77***	7
PACH (M)	52	0.0023	0.059	39	4.23***	6
Vault (n = 24)						
MIKca (F)	26	0.0026	0.084	31	3.28***	17
MIKca (M)	28	0.0034	0.108	31	5.46***	20
MIKsc (F)	17	0.0025	0.081	31	4.94***	25
MIKsc (M)	13	0.0013	0.042	31	2.14***	17
PACH (F)	38	0.0015	0.048	31	1.7**	6
PACH (M)	41	0.0014	0.045	31	1.68*	6
Cranial base (n = 23)						
MIKca (F)	24	0.0018	0.061	29	1.77**	13
MIKca (M)	40	0.0021	0.071	29	2.28***	9
MIKsc (F)	14	0.0018	0.061	29	2.14***	22
MIKsc (M)	13	0.0016	0.055	29	1.56*	21
PACH (F)	47	0.0028	0.075	29	2.12***	8
PACH (M)	49	0.0027	0.093	29	2.45***	10

¹see Table 1 for abbreviations; n, number of landmarks; N, number of specimens.

²Mean square was multiplied by 10³.

³Values were multiplied by 10⁶.

* P < 0.05; ** P < 0.01; *** P < 0.001.

Directional asymmetric changes in the shape of the upper face are displayed in Figure 3. The Mikulčice samples (Fig. 3; a, b, c, d) were similar in terms of shape DA. The midsagittal points, aperthions (APT), and lateral points of the upper face rotated clockwise. The right side of the upper face narrowed relatively in the right-left direction, especially in the lower part. Likewise, the face arch was relatively higher on the right side. The margin of both orbits rotated counterclockwise. The right orbit was relatively lower and wider, whereas the left one was more rounded. Upper face DA in the Pachner Collection (Fig. 3; e, f) was much

less expressed than in the Mikulčice samples. The Pachner Collection exhibited the reverse tendency in the rotation shape of the midsagittal plane and in the shape of the upper face, but a similar tendency in orbital DA. The Mikulčice samples demonstrated a high level of biomechanical stress acting on the right side of the upper face, compared to a low level of biomechanical stress in the Pachner Collection.

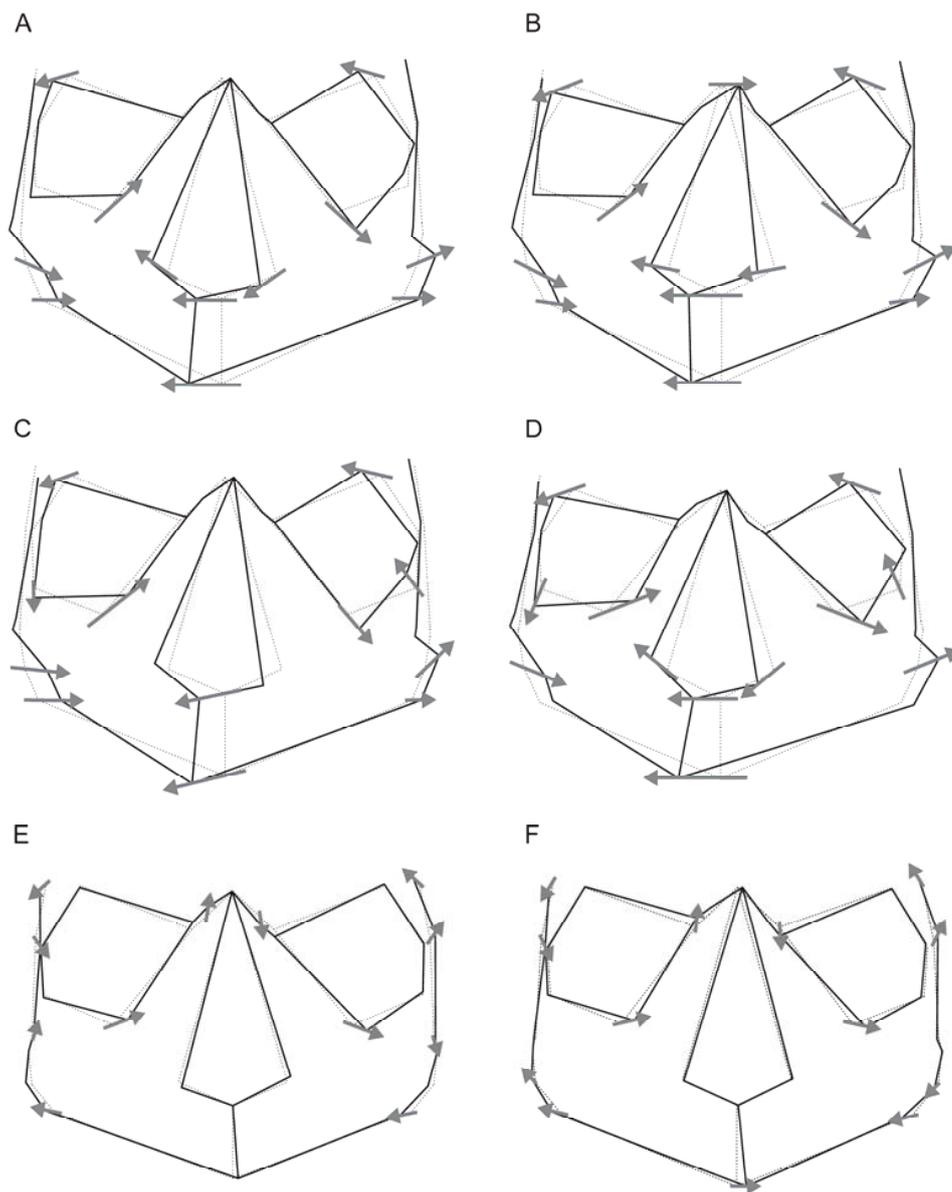


Figure 3. Directional asymmetry of the upper face. Frontal view. Thin links represent symmetric mean shape; bold links link the directional asymmetric changes of each landmark. For better visibility, the observed asymmetry has been exaggerated 3-fold. The black arrows show shifts by directional asymmetry for the 40% of landmarks exhibiting the greatest magnitude.

Shape changes of the vault region due to DA are demonstrated in Figure 4. In this region as well, the crania from Mikulčice were all similar in DA (Fig. 4; a, b, c, d). The right half of the vault was relatively wider, especially in the posterior part, and also higher. The inferior part of the cranium was relatively wider on the left side. In the Pachner Collection, DA was much less expressed than in the Mikulčice samples, but it had a similar tendency

(Fig. 4; e, f), especially in females. The Pachner Collection differed from the Mikulčice samples in the tendency for an anterior shift of the right forehead, together with a posterior movement of the left posterior part of the vault. All samples had a similar tension with a tendency for the right side of the vault, but the expression of DA indicated greater biomechanical loading in the Mikulčice samples.

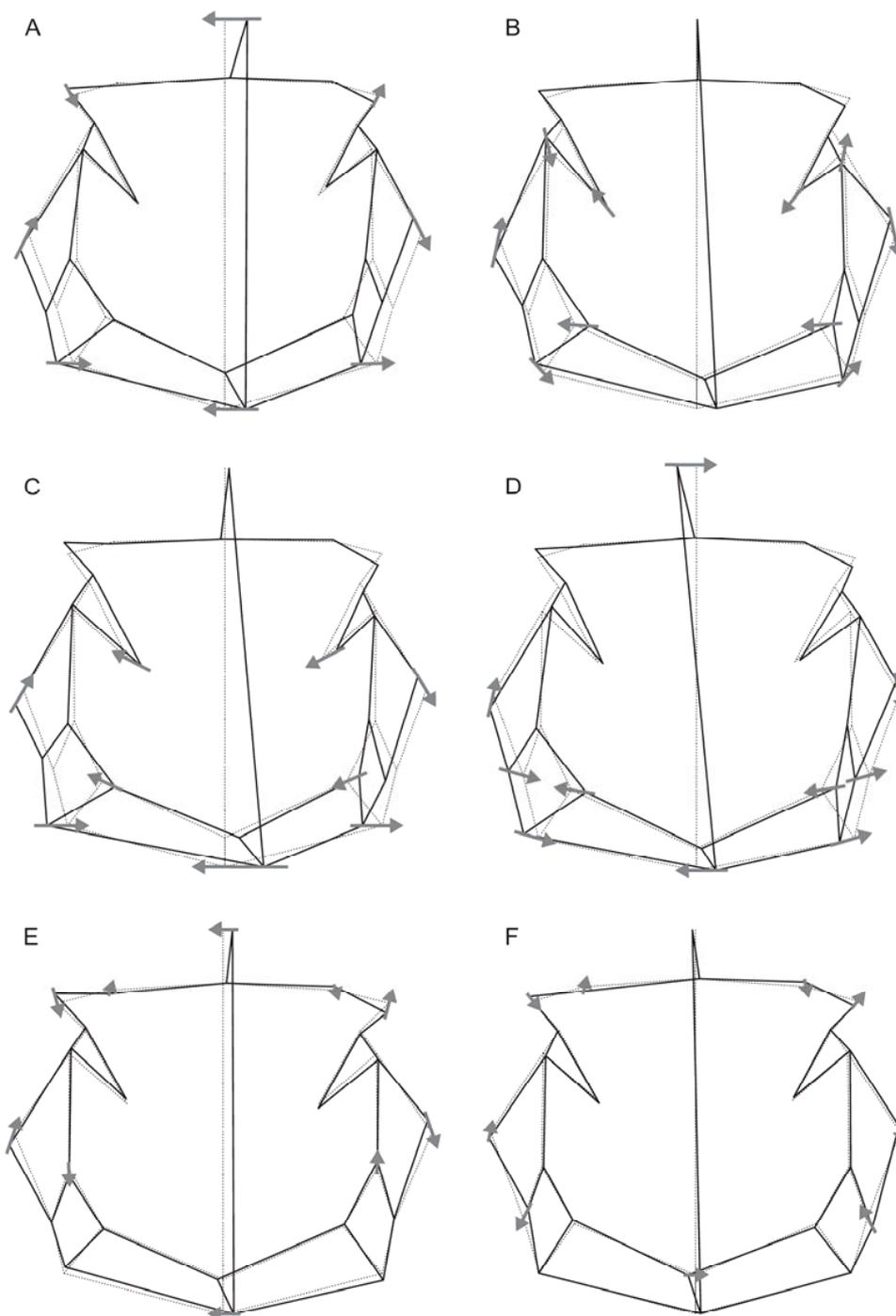


Figure 4. Directional asymmetry of the vault. Superior view. Thin links represent symmetric mean shape; bold links link the directional asymmetric changes of each landmark. For better visibility, the observed asymmetry has been exaggerated 3-fold. The black arrows show shifts by directional asymmetry for the 40% of landmarks exhibiting the greatest magnitude.

Skull Shape Asymmetry of Early Medieval Society

Directional asymmetric changes in the shape of the cranial base are visualized in Figure 5. There was no strong difference between Mikulčice castle (Fig. 5; a, b) and sub-castle (Fig. 5; c, d), nor did the Pachner Collection differ distinctively (Fig. 5; e, f). All of the samples studied showed a similar trend; the left basis was relatively wider, especially in the posterior part. In Mikulčice females, the palate was relatively wider and longer on the left. The cranial base was not affected differently by biomechanical stress between samples.

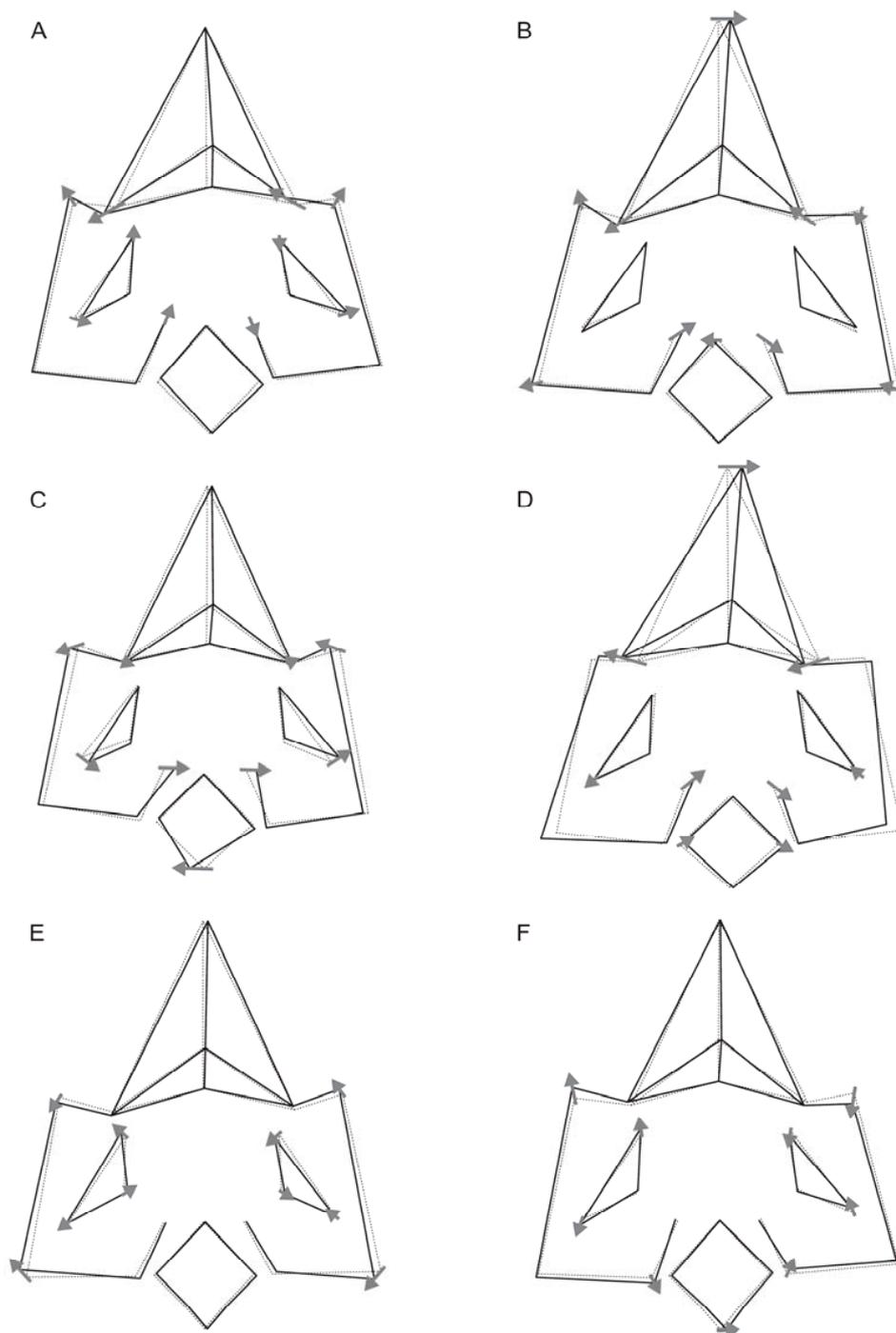


Figure 5. Directional asymmetry of the cranial base. Inferior view. Thin links represent symmetric mean shape; bold links link the directional asymmetric changes of each landmark. For better visibility, the observed asymmetry has been exaggerated 3-fold. The black arrows show shifts by directional asymmetry for the 40% of landmarks exhibiting the greatest magnitude.

Fluctuating asymmetry

The highest mean FA values were attained in the cranial base (0.011), with intermediate values in the vault (0.009), and the lowest in the upper face region (0.006). No significant differences between samples were found in the vault and cranial base. The comparison of FA between samples in the upper face region is presented in Figure 6. Unpaired landmarks were excluded from this comparison, as it reflects the lowest values of FA (DeLeon, 2007). Mikulčice castle females exhibited significantly the highest FA compared to other Mikulčice samples, and exhibited the greatest similarity to the high stressed Pachner Collection (ANOVA: MIKca M, $p < 0.001^{***}$; MIKsc F, $p < 0.000^{***}$; MIKsc M, $p < 0.001^{***}$). Mikulčice sub-castle females exhibited significantly lower FA than Pachner females ($p < 0.001^{***}$). In males, no differences were found between Mikulčice castle and sub-castle. They both attained significantly lower FA than Pachner males (MIKca M, $p < 0.002^{**}$; MIKsc M, $p < 0.002^{**}$). These results were surprising, since on the contrary we had expected Mikulčice castle to be the least stressed compared to other samples, and especially in the case of females.

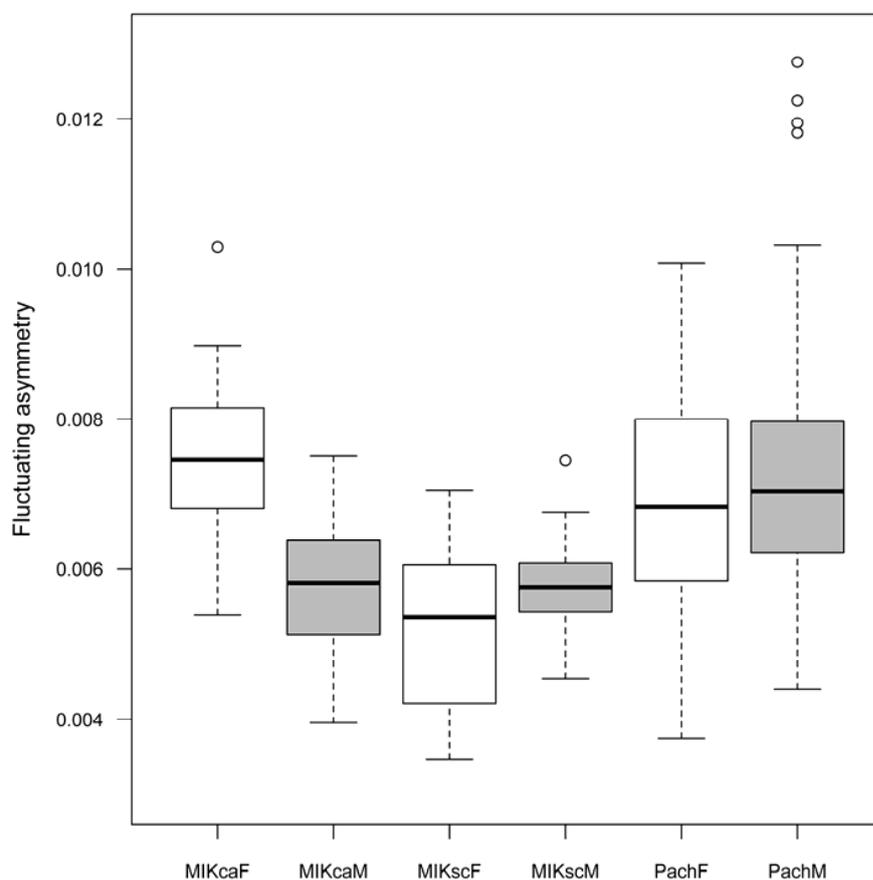


Figure 6. Box-plots of summarized fluctuating asymmetries for the paired landmarks of the upper faces in six monitored samples (see Table 1 for abbreviations).

DISCUSSION

Using directional (DA) and fluctuating asymmetry (FA), we have demonstrated socioeconomic differences between the inhabitants of the castle and sub-castle in the Mikulčice settlement. Differences in craniofacial asymmetry were more distinctive in females, compared to males. Whereas in FA, significant differences were found between

Mikulčice castle and sub-castle in females, so that, surprisingly, Mikulčice castle females were found to be more similar to the high stressed comparative Pachner Collection, males did not differ in any way. By contrast, in DA, significant differences were found not between Mikulčice castle and sub-castle, but between the Mikulčice samples and the Pachner Collection, as was expected. At the same time, the highest DA levels were attained in the upper face region, with intermediate in the vault, and the lowest and the least distinctive in the cranial base.

Our results of the FA assessment confirmed that Mikulčice inhabitants, even from the assumed lower social classes, lived in favorable conditions, as compared to the Pachner Collection, as was already noted (Bodri and Čermák, 1995; Poláček, 2008). In an FA comparison of medieval and modern skulls, Gawlikowska et al. (2007) also noted higher values of FA in the modern sample. The authors ascribed it to the greater influence of developmental stress and a weaker ability for compensation (Gawlikowska-Sroka, 2006; Gawlikowska et al., 2007). In our sample, we hypothesized that FA reflects the greater developmental stress of the lowest socioeconomic group, as the Pachner Collection was characterized as poor people from Prague (Pachner, 1937), who did not have sufficient resources to be buried. Similarly, all other skeletal characteristics indicated that these individuals had been in the lowest socioeconomic position (Borovanský, 1936; Pachner, 1937; Stránská et al., 2005; Kujanová et al., 2008).

A similar result was found by means of a DA evaluation, which confirmed that the Mikulčice inhabitants subsisted on a more solid diet as compared to the Pachner Collection. In all morphological regions, the Mikulčice samples exhibited significantly higher levels of DA than the Pachner Collection, with the greatest being in the upper face. The main factor affecting the DA of this region is the masticatory function (Vig and Hewitt, 1975), but it already appears before dentition (Rossi et al., 2003). Our results confirmed the solid and gritty diet in Mikulčice subsistence. It was already noted that the diet of Mikulčice inhabitants included cereals, as well as pulses and various nuts and fruits (Macháček, 2010). By contrast, the Pachner Collection represents poor people, with an assumed “more liquid” diet (Pachner, 1937), as reflected by the lowest DA values in the upper face. Gawlikowska-Sroka (2006) stated on the contrary that a higher level of DA in the face was typical of modern skulls. When comparing Mikulčice with the Pachner Collection, it is also worth noting that the Mikulčice population was a compact society and the graves came from a relatively long period lasting a century, whereas the individuals from the Pachner Collection were collected over three years and could represent a highly variable sample.

The greatest differences between samples in DA were found in the upper face region, as compared to the vault and cranial base. This was expected, because the upper face region and mandible are the morphological parts of the cranium that most respond to a functional adaptation (Vig and Hewitt, 1975; Shah and Joshi, 1978; Rossi et al., 2003). By contrast, the lowest differences and, at the same time, the lower values of DA, were depicted in the cranial base. Earlier studies also showed that the cranial base is consistent in DA (Kwon et al., 2006). It could be due to the endochondral ossification of the base, which starts early in fetal life. Kohn et al (1995) noticed that cradleboarding did not affect the morphology of the cranial base. It is thus possible that divergent living conditions and even everyday habitual activities do not leave traces in this morphological region.

With regard to direction, the DA of the orbits, vault, and cranial base was similar in the Mikulčice samples and the Pachner Collection, but in the maxilla and cheek bones region, DA exhibited the reverse direction. We suppose that in the cranial base and vault the DA direction reflects asymmetrical brain growth, which develops prenatally (Annett, 2003; Sun and Walsh, 2006). It was reported, that, analogous to our results, the right hemisphere is usually larger in the upper and posterior part and smaller in the basicranial region (Woo,

1931; Hershkovitz et al., 1992; Rossi et al., 2003), and this phenomenon is stable over populations, similar to handedness. The right hemisphere is specified for spatial recognition, the left one is dominant for logical processing and language (Riss, 1984; Geschwind and Miller, 2001). Vault DA is given, according to our results, above all due to the moving of the midsagittal plane. Orbits probably rotated following the vault, but their lower border responded to loading similar to the maxilla and cheek bones (Ercan et al., 2008).

The DA direction of maxilla and cheek bones was similar in the Mikulčice samples. It indicated more a depressed right side of the face, probably in connection with chewing side preference, which was reported in general on the right side (Nissan et al., 2004; Diernberger et al., 2008; Martinez-Gomis et al., 2009). The relative widening of the left side of the upper face also resulted from the rotation of midsagittal landmarks. Some previous studies noted a dominant left side of the face (Woo, 1931; Vig and Hewitt, 1975; McIntyre and Mossey, 2002; Ercan et al., 2008), whereas other describes right side dominance (Farkas and Cheung, 1981; Ferrario et al., 1994, 1995; Shaner et al., 2000). This discrepancy could result from using different methodology (Ercan et al., 2008). In our study, the left side of face was wider, but lower than the right side.

By using a DA comparison, biomechanical loading to support in the upper face region was found to be higher in Mikulčice sub-castle than Mikulčice castle. It indicated differing diets in the Mikulčice samples, which reflects the socioeconomic stratification of past populations (Walker and Hewlett, 1990; Le Huray and Schutkowski, 2005). The grittier diet of lower socioeconomic groups, with the related intense masticatory forces, changes skeletal craniofacial shape more and results in more expressed DA (Greene et al., 1967; Vig and Hewitt, 1975; Carlson and Van Gerven, 1977; Gomes et al., 2011). Similarly, a stable C, N isotope analysis of rich and poor graves from Mikulčice indicated that higher socioeconomic groups had a diet with a greater intake of the much-favored millet and more meat compared to the lower social groups (Smrčka et al., 2008). Divergent diets in higher and lower socioeconomic classes were also supported by a study of caries incidence, which was more evident in poorer graves, as compared to rich graves (Stránská et al., 2008). The authors ascribed it to a greater volume of cereals in the diet of lower socioeconomic groups.

The results showed that differences between Mikulčice castle and sub-castle were more distinctive in females than in males. The comparison of cranial size had already shown higher differences in Mikulčice females than males. Mikulčice castle females exhibited consistently larger linear dimensions of the skull than Mikulčice sub-castle females. Given that a low-protein diet leads to a smaller cranial size (Cohen and Armelagos, 1984; Sardi et al., 2006), we assume Mikulčice castle females to have lived in better conditions with better subsistence. Similarly, the individual asymmetry (IA) comparison between samples indicated higher differences between Mikulčice castle and sub-castle among females, so that Mikulčice sub-castle females exhibited higher IA. It indicated higher differences in biomechanical loading to support in Mikulčice females. Similarly, no statistical differences were found in stature between higher and lower socioeconomic groups in Mikulčice; however, the differences were more distinctive in females (Dobisíková et al., 2008). Females were more affected by caries than males (Stránská et al., 2008).

The most inconsistent differences among Mikulčice females and males were found in the FA comparison. Whereas no differences were depicted between Mikulčice castle and sub-castle in males, females differed significantly. A significantly greater level of FA was found in Mikulčice castle females compared to Mikulčice sub-castle females. Mikulčice castle females thus showed the greatest similarity to the lowest socioeconomic groups of modern society (Pachner, 1937). This result was surprising, since Mikulčice castle females were expected to derive from the highest groups of society (Stloukal and Vyhnánek, 1976; Poláček, 2008) and so to be less affected by environmental stress (Özener, 2010). Simultaneously,

females were reported to be better at overcoming the detrimental conditions, as compared to males (Klein, 2004; Møller et al., 2009). As Havelková et al. (2011) have noted, Mikulčice castle females were more affected by enthesal changes than the assumed lower socioeconomic groups. Females buried in Mikulčice castle were thus possibly derived mostly from lower socioeconomic groups, such as servants or slaves. Fluctuating asymmetry could also increase with rapid morphological change within a population (Kimmerle and Jantz, 2002). So another explanation could derive from the fact that patrilocality was a conventional phenomenon in Early Medieval populations (Ennen, 2001). Females were taken in, which was most conspicuous in higher socioeconomic groups, as females were probably from more distant communes than females from the lower classes of society.

In contrast, no differences in FA were depicted between Mikulčice castle and sub-castle males. They both exhibited the lowest values of FA, similar to Mikulčice sub-castle females. It is possible that in the castle region there were many members of middle and lower society, such as warriors, craftsmen, or servants, buried here side by side with higher classes of the population. Another possibility is that in the sub-castle burial grounds many wealthy people from the vicinity of the residential palace were buried (Poláček, 2008). In total, males exhibited lower values of FA and thus less environmental stress than females, but only from Mikulčice castle. This result is supported by observations made of other medieval societies, where the incidence of enamel hypoplasia, Harris lines, or teeth caries indicates the lower socioeconomic position of women, as compared to men, depending on differing access to food resources (Šlaus, 2000; Esclassan et al., 2009; Lucas et al., 2010).

CONCLUSION

1. Craniofacial asymmetry assessment confirmed socioeconomic differences between Mikulčice castle and sub-castle inhabitants. We also noted the differences as being more expressive among females than among males.

2. Our results confirmed that Mikulčice inhabitants, even from what were assumed to be lower social classes, lived in favorable conditions and subsisted on a more solid diet, compared to the Pachner Collection. Both FA and DA assessment showed great differences between these diachronic samples, in favor of Mikulčice.

3. The dietary differences between socioeconomic groups in Mikulčice were confirmed by DA of the upper face and vault. The greatest differences in DA between samples were found precisely in this region. Mikulčice sub-castle had to support insignificant higher levels of biomechanical stress affecting the upper face and vault, in connection with grittier and more solid foods such as cereals, compared to Mikulčice castle, where there was more meat in the diet. Conversely, the comparative high stressed sample of the Pachner Collection exhibited by far the lowest values of DA in the upper face region. The diet of these poor people probably was more liquid.

4. Differences in asymmetry were depicted in the region of the vault when sex is considered. A similar result was found using cranial size. Whereas males exhibited greater similarity in Mikulčice castle and sub-castle region, in females higher differences existed, so that Mikulčice sub-castle females were smaller and at the same time more directional asymmetric in the vault than Mikulčice castle females. These results supported the hypothesis that males buried in Mikulčice castle and sub-castle were more mixed, coming from higher social classes as well as middle and lower classes. Females buried in Mikulčice sub-castle probably came from lower social classes than the ones buried in the castle. But this result of DA assessment is not supported by FA estimation.

5. Fluctuating asymmetry is an indicator of socioeconomic differences, as it reflects environmental stress and simultaneously it increases with the variability of the population. In

males, no differences in FA were depicted between Mikulčice castle and sub-castle, whereas in females, the differences were significant, with the Mikulčice castle females' tendency for higher values. They exhibited similar FA values as the high stressed Pachner Collection. We expected that it could be by reason of the higher variability among Mikulčice castle females compared to other Mikulčice samples, in connection with the phenomena of patrilocality in early medieval societies.

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Příloha G

Variability of the Early Medieval skulls from Mikulčice (Czech Republic). 3D geometric morphometric comparison with the recent population

Poster. *Iberian Symposium on Geometric Morphometrics*. Barcelona, 23.-25.7. 2009.

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ABSTRACT This study presents an approach for evaluating the variability and diachronic changes of adult skulls using three-dimensional geometric morphometric methods. The study sample consisted of 173 medieval and 136 identified skulls from the first half of the 20th century. The three-dimensional coordinates of 43 ectocranial landmarks and 39 semi-landmarks covering the midsagittal curve of the cranial vault were digitized using a MicroScribe G2X contact digitizer. The set of coordinates were submitted to multivariate (MANOVA) and geometric morphometric methods (GPA, shape PCA and TPS).

The purpose of this study was to monitor diachronic variability in the shape of skulls within the territory of Central Europe from the Early Middle Age until the present. We posed the question whether we can prove that the most typical evolutionary changes of anatomically modern man, the development of neurocranial globularity and decreased facial convexity (Lieberman et al., 2002; Velemínská et al., 2008), can be observed in the medieval-current period. Our argument is based not only on detailed craniometric analysis of the skull as a whole but also on the shape microevolution of the various facial parts of the skull.

The medieval skulls were significantly longer and narrower, in combination with wider faces and foreheads. Their marked facial convexity is produced by a strong protrusion of the upper jaw. Height relations of the faces in the medieval skulls are similar to those in the current Central European population. This observed facial morphology is much less pronounced but similar to the Czech Upper Paleolithic skulls from Předmostí and Dolní Věstonice.



VARIABILITY OF THE EARLY MEDIEVAL SKULLS FROM MIKULČICE (CZECH REPUBLIC)

3D GEOMETRIC MORPHOMETRIC COMPARISON WITH THE RECENT POPULATION

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This study presents an approach for evaluating the variability and diachronic changes of adult skulls using three-dimensional geometric morphometric methods. The study sample consisted of 173 medieval and 136 identified skulls from the first half of the 20th century. The three-dimensional coordinates of 43 ectocranial landmarks and 39 semi-landmarks covering the midsagittal curve of the cranial vault were digitized using a MicroScribe G2X contact digitizer. The set of coordinates were submitted to multivariate (MANOVA) and geometric morphometric methods (GPA, shape PCA and TPS).

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the development of neurocranial globularity and decreased facial convexity (Lieberman et al. 2002, Velemínská et al., 2008), can be observed in the medieval-current period. Our argument is based not only on detailed craniometric analysis of the skull as a whole but also on the shape microevolution of the various facial parts of the skull.

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MATERIAL AND METHOD

MATERIAL

- 1 Early medieval skulls from Great Moravia, Mikulčice (Czech Republic) 173 adult skulls (89 females, 84 males)
- 2 Recent skulls, "Pachner's identified collection" from Prague (Czech Republic) 136 adult skulls without mandibles (73 males, 63 females) - identified (name, sex, age, year of autopsy...)

METHOD

Landmarks and semi-landmarks

- 55 traditional landmarks of regions of the vault, face and cranial base
- 39 semi-landmarks covering midsagittal curve of the vault (from Nasion to Opisthion)

List of landmarks: Medial landmarks: B-bregma, N-nasion; L-lambda; NS-nasospinale; Pr-prosthion; F.inc.-foramen incisivum; Ho-hormion; Ba-basion; O-opisthion

Paired landmarks: Eu-aurium; Co-coronale; Ft-frontotemporale; Ju-jugale; Apt-apertion; Fmt-frontomolare temporale; Fmo-frontomolare orbitale; Mf-maxillofrontale; Ek-ektokochion; Spa-suprakochion; Sbk-subkochion; Zm-zygomaxillare; Ms-mastoidale; Basty-basostylion anterior; FdI-foraminolaterale; LaCo-occipitocondylion laterale; MeCo-occipitocondylion mediale; AntCo-occipitocondylion anterior; PoCo-occipitocondylion posterior; Cam-caroticum; Ovm-ovale mediale; Spi-spinale; It-infratemporale



STATISTICAL METHODS

Data acquisition

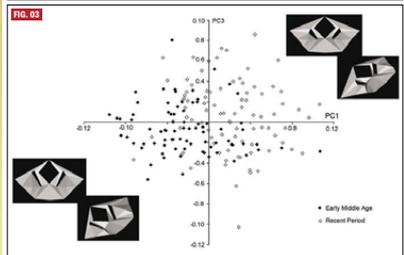
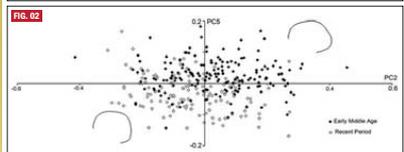
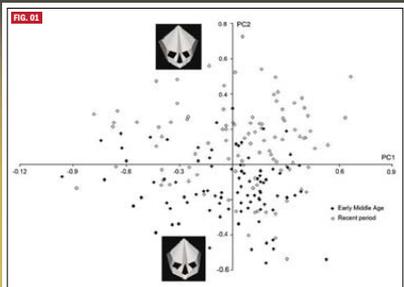
3D co-ordinates were taken by MicroScribe G2X 3D digitizer (Immersion Corp.)

Statistical methods

Generalized Procrustes Analysis (GPA), Principal Component Analysis (PCA), Thin-Plate Splines method (TPS), Multivariate analysis of variance (MANOVA)

Software

Rhinoceros NURBS modelling (McNeel & Associates), Morphologika (by P. O'Higgins & N. Jones), PAST (by O. Hammer, D.A.T. Harper & P.D. Ryan), Morpheus et al. (by D.E. Slice), Avizo 5.0



RESULTS AND CONCLUSIONS

RESULTS

Shape of the skull as a whole (33 landmarks)

PC1, 20.95% var; PC2 13.08% var; MANOVA p=0.002

Differences to recent skulls (Fig. 01, 04):

- wider neurocranium - narrower face - retrusion of maxilla
- lesser convexity of the face - anterior shift of the landmark Opisthion - posterior shift of the landmark Bregma
- inferior shift of the landmark Lambda

Midsagittal curve of the neurocranium (41 landmarks)

PC2, 22.08% var; PC5 4.31% var; MANOVA p=0.002

Differences to recent skulls (Fig. 02):

- more rounded - flatter in parietal and occipital region (Bregma and Lambda region)

Basis of the neurocranium (25 landmarks)

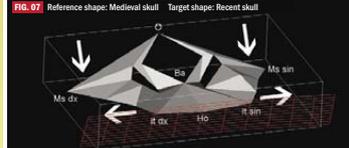
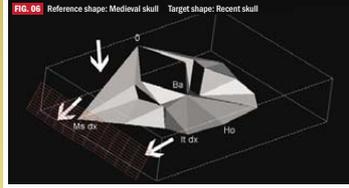
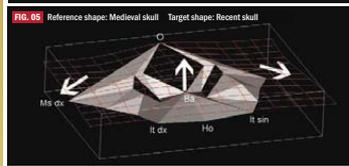
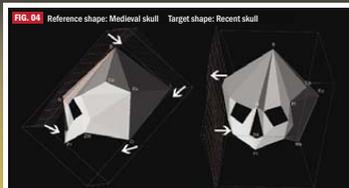
PC1, 17.66% var; PC3 9.25% var; MANOVA p=0.001

Differences to recent skulls (Fig 03, 05-07):

- inferior shift of mastoid region - superior shift of landmark Basion - widening of the distance between infratemporal landmarks - shortening of occipital condyles

CONCLUSIONS

1. The shape of early medieval and recent skulls was significantly different in all the investigated regions (skull as a whole, midsagittal curve of neurocranium, region of orbits, nose and palate).
2. The development of neurocranial globularity and decreased facial convexity can be observed in the medieval-recent period.
3. This observed microevolutionary cranial diachronic changes is much less pronounced but similar to the macroevolutionary cranial changes from the Czech Upper Paleolithic to current period.



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Příloha H

Craniofacial Variability and Diachronic Changes from the Early Medieval to the Recent Period in the Central European population - a 3D Geometric Morphometric Comparison

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ABSTRACT The purpose of this study was to monitor diachronic variability in the shape of skulls within the territory of Central Europe from the Early Middle Age to the present. We posed the question whether we can prove that the most typical evolutionary changes of anatomically modern humans, the development of neurocranial globularity and decreased facial convexity, can be observed in the medieval-current period. Our argument is based on detailed craniometric analysis of the skull as a whole, but also on the microevolutionary morphology of the various facial parts of the skull.

The study sample consisted of 185 medieval and 133 identified skulls from the first half of the 20th century. The three-dimensional coordinates of 10 midline and 15 bilateral ectocranial landmarks were digitized using a MicroScribe G2X contact digitizer. The set of coordinates was submitted to multivariate (MANOVA) and geometric morphometric methods (GPA, shape PCA and TPS).

Over the period from the Middle Ages to recent times the neurocranium shortened and widened and, together with the face and forehead, became narrower. Marked facial flattening is produced by a strong retrusion of the upper jaw. Orbits in recent skulls are more rounded, and the orbit aperture is positioned in a slightly sagittal direction. The nasal aperture is relatively narrower, and the nasal bones are more prominent. The palate is deeper in recent skulls in the region of the os palatinum, but the anterior part is flatter. This observed facial morphology is much less pronounced but similar to the Czech Upper Paleolithic skulls from P edmostí and Dolní V stonice.



Craniofacial Variability and Diachronic Changes from the Early Medieval to the Recent Period in the Central European population a 3D Geometric Morphometric Comparison

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The purpose of this study was to monitor diachronic variability in the shape of skulls within the territory of Central Europe from the Early Middle Age to the present. We posed the question whether we can prove that the most typical evolutionary changes of anatomically modern humans, the development of neurocranial globularity and decreased facial convexity, can be observed in the medieval-current period. Our argument is based on detailed craniometric analysis of the skull as a whole, but also on the microevolutionary morphology of the various facial parts of the skull.

The study sample consisted of 185 medieval and 133 identified skulls from the first half of the 20th century. The three-dimensional coordinates of 10 midline and 15 bilateral ectocranial landmarks were digitized using a MicroScribe G2X contact digitizer. The set of coordinates was submitted to multivariate (MANOVA) and geometric morphometric methods (GPA, shape PCA and TPS).

Over the period from the Middle Ages to recent times the neurocranium shortened and widened and, together with the face and forehead, became narrower. Marked facial flattening is produced by a strong retrusion of the upper jaw. Orbits in recent skulls are more rounded, and the orbit aperture is positioned in a slightly sagittal direction. The nasal aperture is relatively narrower, and the nasal bones are more prominent. The palate is deeper in recent skulls in the region of the os palatinum, but the anterior part is flatter. This observed facial morphology is much less pronounced but similar to the Czech Upper Paleolithic skulls from Předmostí and Dolní Věstonice.

This project was supported by a grant from the Grant Agency of the Czech Republic (GAČR, project 206/07/0699), by research grant MSM 0021620843 from the Ministry of Education, Youth and Sports of the Czech Republic, and by Centralized Development Project C37/3 from the Ministry of Education, Youth and Sports of the Czech Republic.

MATERIAL AND METHOD

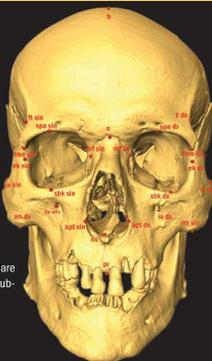
MATERIAL

1 Early medieval skulls from Great Moravia, Mikulčice (Czech Republic); 185 adult skulls (81 females, 91 males, 13 not identified)
2 Recent skulls, "Pachner's identified collection" from Prague (Czech Republic), 133 adult skulls without mandibles (72 males, 61 females) - identified (name, sex, age, year of autopsy...)

METHOD

Landmarks
- 10 midline and 15 bilateral ectocranial landmarks of regions of the skull as a whole, orbits, nasal region and palate

List of landmarks: Medial landmarks: B-bregma; N-nasion; L-lambda; NS-nasospinale; Pr-prosthion; Inc-foremen incisivum; O-opisthion; Sta-staphylion; St-staurion; Rhi-rhinion
Paired landmarks: Eu-eyrium; Co-coronale; Fr-frontotemporale; Ju-jugale; Apt-apertion; Fmt-frontomale temporale; Fmo-frontomale orbitale; Mf-maxillofrontale; Ek-ectocochlion; Spa-supraconchion; Sbk-subconchion; Zm-zygomaillare; Ms-mastoideale; Mnf-maxillonasofrontale; Poa-postalverion

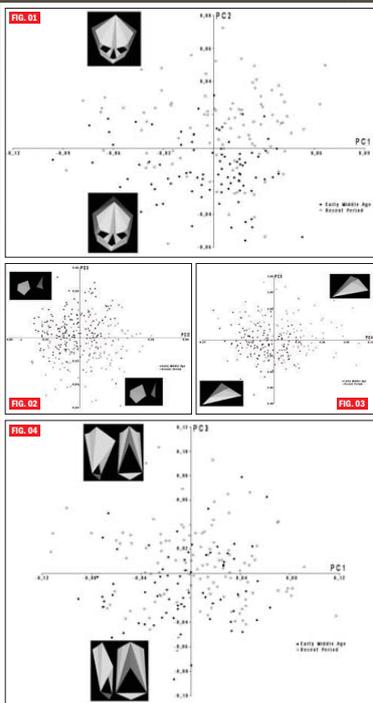
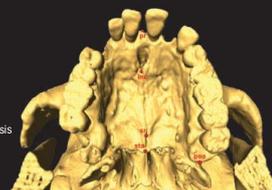


STATISTICAL METHODS

Data acquisition
3D co-ordinates were taken by MicroScribe G2X 3D digitizer (Immersion Corp.)

Statistical methods
Generalized Procrustes Analysis (GPA), Principal Component Analysis (PCA), Thin-Plate Splines Method (TPS), Multivariate analysis of variance (MANOVA)

Software
Morphologika (by P. O'Higgins & N. Jones), PAST (by O. Hammer, D.A.T. Harper & P.D. Ryan), Morphueus et al. (by D.E. Slice), Avizo 5.0



RESULTS AND CONCLUSIONS

Shape of the skull as a whole (33 landmarks)

PC1, 20.95% var; PC2 13.08% var; MANOVA p=0.002
Differences to recent skulls (Fig. 01, 05):
wider neurocranium - narrower face - retrusion of maxilla - lesser convexity of the face - anterior shift of the landmark Opisthion - posterior shift of the landmark Bregma - inferior shift of the landmark Lambda

Orbital region (10 landmarks)

PC2 17.0% var; PC3 13.3% var, MANOVA p=0.001
Differences to recent skulls (Fig. 02, 06):
orbits more rounded - orbit aperture in a slightly sagittal direction - shortening of the distance between orbits

Palate (6 landmarks)

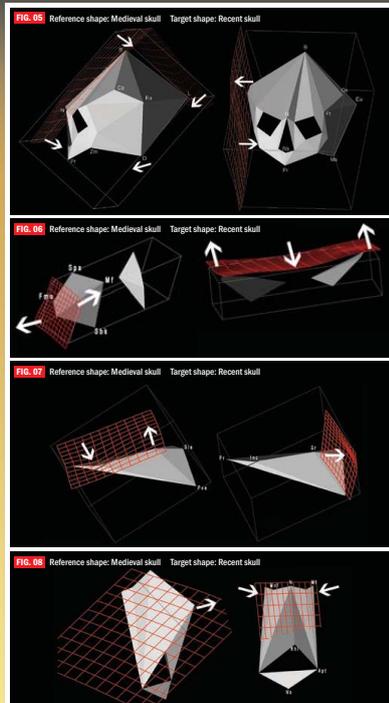
PC4 13.0% var; PC5 5.7% var, MANOVA p=0.002
Differences to recent skulls (Fig. 03, 07):
deeper in the region of the os palatinum - flatter anterior part - posterior shift of the landmark Staphylion

Nasal region (9 landmarks)

PC1 21.4% var; PC3 12.7% var, MANOVA p=0.001
Differences to recent skulls (Fig. 04, 08):
more prominent nasal bones - narrowing of the nasal region

CONCLUSIONS

1. The shape of early medieval and recent skulls was significantly different in all the investigated regions (skull as a whole, region of orbits, nose and palate).
2. The development of neurocranial globularity and decreased facial convexity can be observed in the medieval-recent period.
3. This observed microevolutionary cranial diachronic changes is much less pronounced but similar to the macroevolutionary cranial changes from the Czech Upper Paleolithic to the current period.



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