Istraživanje direkcijske i fluktuacijske asimetrije maksilofacijalnih struktura metofom geometrijske morfomerije

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ISTRAŽIVANJE DIREKCIJSKE I FLUKTUACIJSKE ASIMETRIJE MAKSILOFACIJALNIH STRUKTURA METODOM GEOMETRIJSKE MORFOMETRIJE

DOKTORSKI RAD

Zagreb, 2020.

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Sažetak:

Morfološka asimetrija kao odstupanje od potpune bilateralne simetrije često se koristi za procjenu genetičke i razvojne (ne)stabilnosti organizma. Kako su obje strane bilateralno simetričnog obilježja upravljane jednakim genima, njihova asimetrija nastaje kao rezultat djelovanja različitih remetilačkih faktora tijekom ontogenetskog razvoja. Za proučavanje rasta i razvoja, poremećaja i bolesti poligenskog nasljeđivanja primjerena je populacija koja je reproduktivno i geografski izolirana jer ima ograničeni genski bazen.

Za istraživanje asimetrije lice u ovom istraživanju korištena je populacija otoka Korčule i Visa kao rijedak i vrijedan primjer geografski i reproduktivno izolirane populacije. S druge strane, populacija grada Splita primjer je panmiktične populacije i korištena je kao kontrolna skupina. Za ovo istraživanje koristilo se sveukupno 110 CBCT snimki. Trodimenzionalna rekonstrukcija podataka i trodimenzionalna antropometrijska mjerenja rađena su u softveru Viewbox 4 (dHAL, Greece). Nakon digitalizacije, antropometrijske točke određene su svojim koordinatama (x, y, z) i analizirane su metodama geometrijske morfometrije u programu Mathematica 4.1 (Wolfram Research, Inc., United Kingdom). Totalna, direkcijska i fluktuacijska asimetrija cijelog kraniofacijalnog skeleta, kranija i mandibule nije ovisna o dobi, spolu ili o mjestu stanovanja (Korčula, Split, Vis). Iznosi za totalnu asimetriju općenito znatno su veći za područje mandibule, nego za područje kranija i za totalnu asimetriju. Postoji **direkcijska asimetrija** cijelog kraniofacijalnog skeleta, kranija i mandibule kod svih triju skupina ispitanika..Ispitanici s područja Visa imaju najveći iznos direkcijske asimetrije za cijelo područje kraniofacijalnog skeleta i kranija. Ispitanici s područja Korčule imaju najveći iznos direkcijske asimetrije mandibule. Iznos direkcijske asimetrije najmanji je za mandibulu za sve tri skupine ispitanika. Iznosi **fluktuacijske asimetrije** za područje kranija veći su od fluktuacijske asimetrije mandibule. Vektorskom analizom smjera fluktuacijske asimetrije u odnosu na dob vidi se kako su promjene smjera izraženije u skupini ispitanika starijih od 55 godina i to dominantno u nazo-orbitalnom području

Dobne promjene oblika kraniofacijalnog skeleta veće su kod ispitanika ženskog, nego kod ispitanika muškog spola. One imaju stalnu uzlaznu promjenu, no nakon 55 godina krivulja promjene oblika kraniofacijalnog skeleta u ovisnosti o dobi kod ispitanika ženskog spola postaje diskontinuirana s nepredvidljivim uzlaznim i silaznim varijacijama.

Ključne riječi: facijalna asimetrija, fluktuacijska asimetrija, direkcijska asimetrija, geometrijska morfometrija, izolirana populacija, CBCT

Extended summary

Introduction

Developmental processes are extremely complex processes that lead to the creation of a final or current phenotype. Due to their extreme complexity, a perfectly regular and symmetrical process is almost impossible to achieve. The balance of all processes with the interaction of external environmental factors implies the achievement of full functionality of the system with primary or secondary morphological construction. Such construction in its course leaves on the morphology of the organism small markers that can serve as an indicator of certain factors of development, both environmental and genetic (1).

The growth and development of the human craniofacial system is under significant control of genetic factors, i.e. under the influence of certain groups of genes whose activation and expression are well programmed. Control genetic mechanisms are largely non-specific in nature, such as regulatory genes that act not only on the craniofacial system, but on the whole organism. On the other hand, there are very specific control patterns of development that establish a species-specific physiognomy with relatively small morphological variations. Although human face variations appear to be large, they are actually minimal given the complexity of the development cycle (2).

Different parts of the face have different development in terms of time, speed and direction of growth and development (3). A significant role in the duration of these processes, as well as in lifelong changes is played by different hormonal interactions and the time of action and concentration of individual hormones, which, each with its own complete or additive effect, contributes to the change of morphological characteristics of the face.

Asymmetry is a deviation from the identical shape or size of two sides of the body. It is one of the most common facial features. Due to the lack of use of the mid-sagittal plane, mirror object modelling can provide the most accurate assessment of craniofacial asymmetry.

It is widely believed that increased asymmetry indicates the failure of the organism to maintain developmental homeostasis and the overcoming of environmental disorders over genetic control mechanisms (4). Developmental stability means the body's resistance to various disorders that can affect the body during growth and development, and we can express it by slight random deviations from bilateral symmetry (5). Since fluctuating asymmetry is caused by the inability of the organism to allow the left and right sides to develop equally, it is often used in research as a measure of developmental instability that

occurs during the development of the organism (6, 7). If an environmental factor changes, the result is a change in directional asymmetry because this stress acted on both the left and right sides of the body, as a developmental response to environmental factors, depending on positional signals regulating the differences between left and right. Therefore, the variation of directional asymmetry with developmental factors is a special example of a reaction norm, something that affects both sides of the body.

Considering that the significant role of heredity in facial development has been pointed out so far, a study of the developmental stability of the facial phenotype would indicate the relationship and interaction of genetic and environmental factors during the growth and development of the craniofacial system.

Despite the overall low level of differentiation in the human population, local factors such as geographical and cultural isolation can greatly affect genetic discontinuity. Clearly distinguished genetic isolates are very valuable for mapping rare and elucidating the mechanism of occurrence of complex genetic diseases (8). Therefore, this study of the asymmetry and shape of the craniofacial skeleton was conducted on an isolated population of Croatian Dalmatian islands and on a panmictic (non-isolated) population of the city of Split.

Aim of the study

The aims of the study were:

1. To calculate the amounts of total asymmetry of the entire craniofacial skeleton, cranium and mandible and determine whether they are grouped by age and sex and study them in a group of subjects from the area of Korčula, Vis and Split.
2. To determine whether there is direct asymmetry of the entire craniofacial skeleton, cranium and mandible in the group of subjects from the area of Korčula, Vis and Split and, if so, whether there is a difference between these groups and what is its direction.
3. To determine whether there is a fluctuating asymmetry of the entire craniofacial skeleton, cranium and mandible in the group of subjects from the area of Korčula, Vis and Split and, if so, whether there is a difference between these groups and what is its direction.
4. To determine the existence of sex and age differences in the form of the craniofacial skeleton and depending on the place of residence of the subjects (Korčula, Split, Vis).

Sample and methods

The studied population of the islands of Korčula and Vis is a rare and valuable example of a geographically and reproductively isolated population. On the other hand, the

population of the city of Split is an example of a panmictic population. Since it shares most of the environmental factors with the population of Vis and Korčula, the population of the city of Split was used as a control population. This group is representative of a mixed and non-isolated population.

A total of 110 CBCT images were used for this study. Out of the total number, 46 images belong to the inhabitants of the island of Vis, 15 to the inhabitants of Korčula, and 49 images belong to the population of the city of Split. All images were taken with the same CBCT device (Scanora 3D, Soredex, Finland) and belong to the Project database. All images are of the same dimensions, field size (FOV) 10 x 14.5 cm, isotropic voxel size 0.25 mm with a total of 300 projection images per subject. The images were stored in the Digital Imaging and Communication in Medicine (DICOM) format.

Three-dimensional data reconstruction and three-dimensional anthropometric measurements were performed in Viewbox 4 software (dHAL, Greece).

After loading the three-dimensional image and showing the craniofacial skeleton, the region of interest for each subject was determined individually. It included the entire craniofacial complex, the cranium from the upper bone edge of the left and right orbits to the lower edge of the maxilla, and the entire mandible.

The following anthropometric points in the mid-sagittal plane were used: prosthion (pr), anterior nasal spine (sna), posterior nasal spine (snp), incisive foramen (fi), linguale (lng) and infradentale (id). The paired points were: orbital (or), pyriform aperture (ap), zygoorbital (zo), zygomaxillare (zm), mandibular foramen (fma), mental foramen (fme) and coronoid (cn). After digitization, the anthropometric points were determined by their coordinates (x, y, z) and analysed by geometric morphometrics in Mathematica 4.1 (Wolfram Research, Inc., United Kingdom).

The following methods were used to analyse the shape and symmetry of the craniofacial skeleton: General Procrustean method of superposition (for standardization of object size), modelling of an image of an object, and principal components analysis (PCA) (9).

Mathematical procedures for determining the total asymmetry were performed according to Mardia et al. (10). The degree of individual morphological asymmetry was calculated as the difference in shape (Procrustean distance) between the configuration of the face and its mirror reflection. The first determined total asymmetry (total asymmetry - TA) of the sample was divided into directional asymmetry (DA) and fluctuating asymmetry (fluctuation asymmetry -

FA). The principal components analysis (PCA) indicated the distribution of dominant shape variations within different populations and presented the main differences between them (11). Differences in asymmetry amounts were checked by analysis of variance (ANOVA).

Results

Total asymmetry

The total asymmetry for the area of the entire craniofacial skeleton as well as for the cranium and mandible expressed in units of Procrustes distance is not grouped according to age or sex.

ANOVA showed that there was no statistically significant difference (R^2= 0.094) in the amount of total asymmetry neither by age and sex of the subjects, nor by place of residence (Vis and Korčula), nor by the amount of inbreeding.

Subjects from the area of Korčula differ statistically significantly in the amount of total asymmetry for the area of the mandible compared to the subjects from Vis and Split.

Directional asymmetry

The difference in asymmetry between the sexes and between populations depending on the place of residence has not been established. The amount of directional asymmetry is the smallest for the mandible for all three groups of subjects. Subjects from the area of Vis have the highest amount of directional asymmetry for the entire area of the craniofacial skeleton and for the area of the cranium, and subjects from the area of Korčula have the highest amount of directional asymmetry of the mandible. Changes in the direction of directional asymmetry after the age of 55 are visible in all subjects in the orbital and nasal area, while changes in the mandibular area are noticeably small. Changes in the direction of directional asymmetry do not intensify with age. The largest changes are shown by the pyriform aperture point in subjects younger than 55. As the aperture rotates counter clockwise, the right one moves laterocaudally and the left one moves mediocranially.

Fluctuating asymmetry

There was no statistically significant difference in the amount of fluctuating asymmetry, neither by age and sex of the subjects, nor by place of residence (Vis and Korčula), nor by the amount of inbreeding. Changes in the direction of fluctuating asymmetry are visible in all subjects on the entire craniomandibular skeleton. Changes in the direction of

fluctuating asymmetry are more pronounced in subjects older than 55. The largest changes are visible in the zygoorbital, nasal, and coronoid areas.

Shape analysis

An F test showed that there was a statistically significant difference in the shape of the craniofacial skeleton between female and male subjects (p= 0.025).

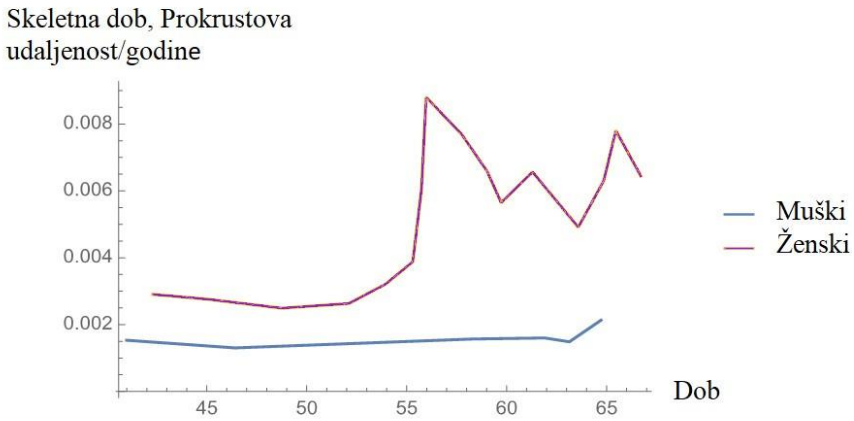

Image 1. Dependence of the change in the shape of the craniofacial skeleton in relation to age in male and female subjects

Changes in the shape of the craniofacial skeleton are greater in female subjects than in male subjects. After the age of 55 (Image 1), the curve of the change in the shape of the craniofacial skeleton in female subjects, which is age-dependent, has a pronounced ascending trajectory, after which it becomes discontinuous with unpredictable ascending and descending variations.

The trajectory curves of men and women are approximately parallel until approximately 55 years of age when in women, the pattern of aging changes and changes in the shape of the craniofacial skeleton caused by aging occur.

Changes in the shape of the craniofacial skeleton in female subjects are more intense than changes in male subjects. In contrast to the intensity, the directions of changes in the shape of the craniofacial skeleton in relation to age in male and female subjects are similar.

Changes in the coronoid, anterior nasal spine, and posterior nasal spine points caused by increasing age occur only in female subjects.

Although the subjects are not grouped into clusters according to their place of residence (Korčula, Split, Vis) and there are many overlaps in the shape of the craniofacial skeleton, the F test showed that there is a statistically significant difference in the shape of the craniofacial skeleton between Korčula and Vis.

Discussion

The results of this study showed that total asymmetry is not grouped by age or by sex. This is in contrast to studies (12, 13) that have shown that the asymmetry of the human face differs between the sexes, its size is age-dependent and is greatest earlier in life. These findings are in agreement with the Rotterdam study (14) in which total and fluctuating asymmetry are significantly related to age and sex. The reasons for these contradictory findings, and taking into account that the asymmetry decreases with age, may lie in the different age structure of the examined populations, i.e. the older age structure of the island population that was the subject of this study.

The results of this study showed that the amount of direct asymmetry is the smallest by several times for the area of the mandible for all subjects, which leads us to the conclusion that the influence of genotype in these subjects on the area of the mandible is the smallest and that all causes of fluctuating asymmetry of the mandible in this population should be considered as environmental impact. As the amount of fluctuating asymmetry of the mandible is the largest for the area of Split, it is inferred that the environmental impact of the city of Split is strong. The amounts of both total and fluctuating asymmetries of the mandible are smaller than that of the cranium, which generally indicates that the environment has less of an impact on asymmetry of the mandible and that the impact on the cranium is much stronger. The total asymmetry of the mandible is statistically significantly lower in the subjects from the Korčula area, and at the same time, the direct asymmetry in this population is the largest, which means that the amount of the total asymmetry is actually directional and that the asymmetry of the mandible in the Korčula area is almost not at all under environmental impact and that the environmental impact on the onset of asymmetry the mandible in subjects from the area of Vis and Split is much higher.

As the largest amounts of Directional asymmetry in the entire craniofacial area, area of the cranium and mandible are divided between island populations, we can think in the direction of a stronger genetic influence on the phenotype of both populations, by comparing them with the population of the city of Split. As the Functioning asymmetry of the mandible is the largest for the area of Split, environmental impact is the greatest and this is in complete contrast to the impact on the asymmetry of the mandible in subjects from the area of Korčula. Functioning asymmetry for the entire craniofacial skeleton and the cranium is the largest in subjects from the area of Vis which also shows a strong environmental impact. This environmental impact, which is obviously stronger in the area of Vis and Split in relation to the more isolated population of Korčula, mutually competes and leads to the total asymmetry of the cranium and mandible being the largest in the area of Vis, but is greatest for the entire craniofacial area in subjects from the area of Split. All this leads us to the following conclusions: the environmental impact on the formation of asymmetry is strong and it has made the populations of Split and Vis similar despite their genetic differences. Microclimate, the specificities of environmental factors, i.e. their weak influence and isolation in the area of Korčula made the specificity of the genotype manifest itself as the smallest total asymmetry of the mandible. It is correct to view these results through a prism of age, since it is an older population, when the influence of genetics, although still effective, decreases and the influence of environmental factors increases. As the influence of environmental factors is obviously small on Korčula, all mandibular asymmetry, although statistically significantly small, should be viewed in the light of purely genetic influence.

Observing the direction of directional asymmetry in the subjects of this study, larger changes in the orbital and nasal area are visible in all three groups (Korčula, Split, Vis), while changes in the mandible are noticeably small, which is expected compared to numerical data. Furthermore, comparing the difference in the amount of directional asymmetry with aging, we see that there are no significantly different changes in directional asymmetry with regards to age, which is consistent with the fact that the largest changes in directional asymmetry are seen at early stages of development. Changes in the direction of individual points as a consequence of directional asymmetry can be interpreted as genotype responses to age-related changes in the craniofacial skeleton. The greatest changes are shown by the pyriform aperture point, with the aperture rotating counter clockwise, the right one moving laterocaudally, and the left one mediocranially. These changes lead to a distortion of the nasal section to the right.

As this one, most previous studies on fluctuating asymmetry is based on a comparison of endogamous, often isolated populations with more exogamous (15, 16, 17). The degree of heterozygosity is associated with lower levels of organizational asymmetry and reflects an increased ability to alleviate genetic and environmental stressors. The higher the degree of heterozygosity in genes encoding proteins or at associated loci (non-random association), the more a better adapted individual is protected from the disorder.

In this context, three hypothetical mechanisms are proposed: 1) a “direct effect” effect according to which heterozygosity increases the ability of the multilocus and may result in functional dominance at the locus *per se* (18, 19). It is also possible that heterozygotes possess enzymes with different catalytic properties and are therefore more biochemically efficient than homozygotes (20). 2) the “local effect hypothesis” suggests heterozygosity as an additional dominance when there is a genetic link (link imbalance) between the neutral marker and the marker under selection (18, 21). And 3) the “general effect” hypothesis states that the advantage of heterozygotes is such that the markers that are detected, which arise from the homozygosity interaction, are loci distributed throughout the genome. A prerequisite for this is that the marker and loci are in the service of identity imbalance which is recorded as the inbreeding coefficient of individuals. A higher inbreeding coefficient means higher marker homozygosity and locus binding ability, while a lower coefficient is associated with heterozygosity and poorer marker-locus link (22,23). As the high degree of inbreeding between subjects in this population was shown in several studies within the Project, and as facial fluctuating asymmetry cannot be related to kinship, it seems that the correlation of heterozygosity and locus ability in this study cannot be explained by these three models and requires additional identification. The same is the case with the Rotterdam study. One possible explanation is Chapman et al. who showed that even if there are correlations in heterozygosity and locus binding ability, they are very small (usually less than 1% of phenotypic variance) (22). Furthermore, the degree of heterozygosity may, on average, be low enough to significantly affect developmental pathways. It is also reasonable to assume that the environment of an island population does not fluctuate enough to make homozygosity unfavourable. The third reason relates to the relative genetic effect on facial asymmetry compared to environmental stressors that accumulate over time.

Conclusions

The conclusions of this study are:

1. The total asymmetry of the entire craniofacial skeleton, cranium and mandible expressed in does not depend on age, sex or place of residence (Korčula, Split, Vis). The amounts for total asymmetry are generally considerably higher for the area of the mandible than for the area of the cranium and for total asymmetry.
2. There is directional asymmetry of the entire craniofacial skeleton, cranium, and mandible in all three groups of subjects. Vector analysis of directional asymmetry showed larger changes in the orbital and nasal areas, while changes in the mandibular area were noticeably small. There is no statistically significant difference in the amount of directional asymmetry for all three observed areas between the groups of subjects from the area of Korčula, Vis and Split. Subjects from the area of Vis have the highest amount of directional asymmetry for the entire craniofacial skeleton and cranial area. Subjects from the area of Korčula have the highest amount of directional asymmetry of the mandible. The amount of directional asymmetry is the smallest for the mandible for all three groups of subjects.
3. There is fluctuating asymmetry of the entire craniofacial skeleton, cranium and mandible in all three groups of subjects (Korčula, Vis, Split), but there is no statistically significant difference between them as in relation to age or sex. The amounts of fluctuation asymmetry for the area of the cranium are greater than the fluctuating asymmetry of the mandible. Vector analysis of the direction of fluctuating asymmetry in relation to age shows that changes in direction are more pronounced in the group of subjects older than 55, and predominantly in the naso-orbital area.
4. Age-related changes in the shape of the craniofacial skeleton are greater in female subjects than in male subjects. They have a constant upward change, but after 55 years the curve of the change in the shape of the craniofacial skeleton as a function of age in female subjects becomes discontinuous with unpredictable upward and downward variations.

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1. UVOD

Rast organizma definiramo kao povećanje veličine ili broja stanica te povećanje međustanične stvari udvostručenjem genetičkog materijala. Pod pojmom razvoja podrazumijevamo, uz rast, udruženu diferencijaciju i translokaciju tkiva. Razvoj je kvalitativna promjena koja obuhvaća promjene u građi, diferencijaciji, morfogenezi, sazrijevanju i prilagodbi tkiva, organa i organizma u cjelini. Vrlo su često ova dva pojma udružena, jer se paralelno odvijaju procesi povećanja veličine i/ili broja stanica i međustanične tvari uz diferencijaciju i translokaciju tkiva. Procesi rasta i razvoja iznimno su složeni procesi koji uključuju velik broj različitih stanica, biokemijskih spojeva, impulsa iz genetičke strukture i okoliša koji zajednički dovode do stvaranja konačnog fenotipa. Zbog iznimne složenosti i kompleksnosti ovih procesa savršeno pravilan i simetričan proces gotovo je nemoguće postići. Ravnoteža svih procesa uz međudjelovanje vanjskih okolišnih čimbenika podrazumijeva postizanje potpune funkcionalnosti sustava uz primarnu ili sekundarnu morfološku izgradnju. Takva izgradnja u svom tijeku ostavlja na morfologiji organizma sitne biljege koji nam mogu poslužiti kao pokazatelj pojedinih čimbenika razvoja, kako okolišnih tako i genetičkih (1).

1.1. Osnove simetričnog i uravnoteženog rasta

1.1.1. Embrionalni i fetalni rast

Organizacija i kompleksnost rasta i razvoja ljudskog organizma jasno se mogu vidjeti već u prvim danima intrauterinog razvoja. Prenatalni kraniofacijalni rast je visoko kompleksni fenomen koji se odvija kroz tri razvojna stadija: stadij jajašca (do 8. dana intrauterinog života (IUŽ)), embrionalni stadij (od 2. do 8. tjedna IUŽ) i fetalni period (od 9. tjedna do rođenja).

Diferencijacija od zigote do fetusa obuhvaća selektivno aktiviranje i represiju diploidnog angažmana gena koji se nalaze u svakoj stanici. Osim toga obuhvaća: translaciju proteina, selektivne mehanizme stanične membrane te različitu intercelularnu aktivnost koja se događa pod metaboličkim, prehrambenim i hormonskim utjecajima. Proces diferencijacije završava citodiferencijacijom i histodiferencijacijom što rezultira stvaranjem epitelnog i mezenhimalnog tkiva. Interakcijom ovih dvaju tkiva započinje organogeneza, tj. konačan razvoj organa i organskih sustava.

Skoro sva tkiva lica i vrata potječu iz ektoderma i većina tkiva razvija se od stanica neuralne kreste koje migriraju prema dolje pored neuralne cijevi i lateralno ispod površinskog

ektoderma. Kada stanice neuralne kreste dovrše migraciju, rastom lica dominiraju regionalni centri rasta (2).

Većina anatomskih struktura glave i vrata nastaje iz ždrijelog luka, parne, duguljaste izbočine mezenhima koji nastaje tijekom 4. i 5. tjedna embionalnog života u razini ždrijelnog crijeva. U početku razvoja nastaje šest ždrijelnih lukova koji su poredani jedan ispod drugog, u kraniokaudalnom smjeru i označuju se brojevima. Tijekom razvoja bujajuće mezodermalne stanice dijele se na anteriornu i posteriornu struju. Iz anteriorne struje formira se frontonazalni nastavak, a iz posteriorne struje razvijaju se dva para maksilarnog i mandibularnog nastavka (2). Ektoderm koji nastaje između nastavaka formira udubljenje stomatodeuma (primitivne usne šupljine). Frontonazalni nastavak nalazi se s gornje strane stomatodeuma, dok se po jedan maksilarni nastavak nalazi lijevo i desno na gornjoj bočnoj strani, a po jedan mandibularni nastavak ispod njih, na donjoj bočnoj strani. Rastom frontonazalnog nastavka prema gore nastaju tri dijela čijim rastom nastaju očne plakode i nazalne jamice, dok rastom prema dolje nastaju dva globularna nastavka čijim spajanjem nastaju: vrh nosa, kolumela, filtrum gornje usne, tuberkulum i frenulum gornje usne, cijelo primarno nepce te premaksila. Posebno treba naglasiti značaj razvoja premaksile iz frontonazalnog nastavka i njezinu relativnu odvojenost u ranoj fazi razvoja od maksilarnih nastavaka što će se ogledati i kasnije, tijekom djetinjstva i imati poseban značaj u praćenju i predviđanju rasta i razvoja gornje čeljusti i srednje trećine lica (3).

Na mjestima spajanja frontonazalnog i maksilarnih nastavaka nastaje nazolakrimalni kanal, također vrlo važna struktura za kasniji rast i razvoj srednje trećine lica, struktura preko koje se odvija klizanje koštanih segmenata i oblikovanje konačnog izgleda lica.

Iz maksilarnih nastavaka nastaju obrazi i lateralni dijelovi gornje usne. Prvi centar osifikacije nazalne i lakrimalne kosti, bilateralno premaksile i maksilarnog nastavka nastaje od hrskavice nazalne kapsule koja se nastavlja na hrskavicu kranijalne baze. Od maksilarnog nastavka nastaje pterigoidni pleksus i veliko krilo sfenoidne kosti, vomer, maksilarni nastavak i palatinalna kost.

Osnova za donju čeljust nastaje rastom i međusobnim spajanjem mandibularnih nastavaka. U 6. tjednu formira se hrskavična tvorba (Meckelova hrskavica) koja se proteže od ušne kapsule do simfize. Iz nje nastaju kondil, mišićni nastavak donje čeljusti te dio kosti oko mandibularnog kanala. Hrskavica ima najveći potencijal okoštavanja i najvažniji je osifikacijski centar rasta mandibule. Preostali dio mandibule okoštava intramembranozno.

Donja usna nastaje od mandibularnog nastavka i dijela koji se nalazi ispod labiolingvalnog sulkusa (2).

Neurokranij i kranijalna baza razvijaju se zajedno kao mezenhimalna ovojnica oko primitivne neuralne osnove i njihov razvoj prati rast centralnog nervnog sustava (CNS-a). Neurokranij kao vezivna ovojnica obavija veliki mozak i okoštava intramembranozno iz više primarnih osifikacijskih centara (čeoni, parijetalni, temporalni, okcipitalni). Rastom tih centara nastaje kranij, a rast mozga stimulira vezivo sutura na staničnu aktivnost i umnažanje. Suture postaju centri kasnijeg rasta. Kranijalna baza razvija se u obliku hrskavične ploče kroz koju prolaze živci i krvne žile baze mozga te okoštava enhondralno. U mediosagitalnoj liniji od kranijalne baze spušta se hrskavični nastavak koji će biti osnova za nosni septum. Njegova stanična aktivnost još će dugo vremena biti važna za rast lica i jedan je od glavnih pokretača rasta nazomaksilarnog kompleksa. Iza septuma je vezivna ploča iz koje će kasnije nastati vomer. U somitskom periodu oko neuralne cijevi mezenhimalnom kondenzacijom razvijaju se 2 sloja: vanjski (ektomeninks) iz kojeg se razvija dura mater i kosti kranijalne baze te unutarnji (endomeninks) iz kojeg se razvija pia mater i anahnoidalna membrana. Sve kosti svoda lubanje osificiraju intramembranozno, dok kosti baze osificiraju enhondralno (4). Primarne funkcije lica (vid, njuh i sluh) razvijene su do poroda, a razvoj intrakranijalnog živčanog sustava prethodi razvoju lica. Stoga je razvoj lica u najranijoj dobi neposredno vezan uz razvoj baze mozga i osjetnih organa vida, njuha i sluha. Rođenjem se mijenjaju funkcije nazomaksilarnog kompleksa pa meka tkiva vezana uz funkcije žvakanja i disanja počinju sudjelovati u razvoju kraniofacijanog sustava. Maleno tijelo novorođenčeta nema velike funkcijske zahtjeve za hranjenje i disanje pa se njegove skeletne jedinice mogu razvijati postnatalno. Enlow navodi da se vremenski period potreban za razvoj povećava s udaljenosti obilježja od neurokranija pa donja čeljust počinje s rastom kasnije i traje duže od srednjeg dijela lica ili očnih duplja (orbita) (5).

1.1.2. Opći principi kraniofacijalnog rasta

Kraniofacijalni sustav glave sastoji se od neurokranija i viscerokranija. Njihova koštana osnova temeljni je morfo-fenotipski čimbenik, a na njega utječu brojni mehanizmi. Koštani sustav raste depozicijom i resorpcijom koje se događaju na poljima rasta i površinskim endosealnim i periosealnim rastom. Polja rasta su sve koštane površine, unutrašnje ili vanjske, koje rastu i nasuprot toga se resorbiraju. Rast se također odvija i pod

utjecajem mekih tkiva (osteogene membrane) i hrskavica. Zbog toga kost, ovisno o mjestu i funkciji (npr. kost uz ligamente, suture ili kost u kojoj se nalaze zubi), ima i različit oblik. Nisu sva polja rasta aktivna u isto vrijeme, najčešće se međusobno nadopunjuju, a neka su samo resorptivna što ima posebno velik značaj na promjenu oblika. Polja rasta koja imaju značajnu ulogu u procesu rasta nazivaju se mjesta rasta (npr. kondil), a mjesta rasta koja su vrlo aktivna nazivaju se centri rasta (suture, kondil, hrskavica nazalnog septuma, sinhondroze, kranijalna baza) (6).

Ovisno o rasporedu polja rasta jedna površina kosti je resorptivna, a nasuprot nje odvija se apozicija kosti. Ako su resorpcija i apozicija uvijek isti i debljina kosti bit će ista.

Ovim osnovnim mehanizmima rasta kost se tijekom rasta pomiče u sve tri dimenzije. Neke kosti koje imaju oblik luka (nepce, mandibula i zigomatični luk) rastu i pomiču se po principu slova „V“. To znači da se apozicija nove kosti odvija na unutarnjoj strani slova V, a resorpcija na vanjskoj. Smjer kretanja, odnosno rasta je prema širokom otvoru slova V. Svi ostali pomaci događaju se u smjeru površine kosti gdje se odvija apozicija što se naziva primarna translacija. Kost se i sekundarno može translatirati kao posljedica rasta okolnog tkiva, odnosno rasta susjedne kosti. Što je kost udaljenija od središta koštanog rasta, izloženija je translacijom pomaku, tj. ti dijelovi bit će više translacijski nošeni.

Uz navedene promjene, u svakoj kosti stalno se odvija i unutrašnja remodelacija koja se sastoji od dvaju simultanih procesa - apozicije (stvaranje nove kosti) i resorpcije (razgradnje postojeće kosti). Njezina je uloga stvaranje i mijenjanje volumena kosti uz održavanje njezine forme (mijenja se regionalno oblik, dimenzija i proporcija). Ovi su postupci osnova rasta i razvoja, odvijaju se zajedno i dio su procesa okoštavanja. Polja remodelacije su veća što je kost veća, ali obrazac distribucije resorptivnih i depozitornih polja se ne mijenja, polja se jedino mijenjaju iz jedne pozicije u drugu, ali broj tijekom života ostaje isti.

Funkcije remodelacije su promjena veličine kosti, relokacija pojedine komponente dopuštajući ukupno povećanje, promjena oblika kosti kao prilagodba na različite funkcije, prilagođavanje kostiju međusobno i u odnosu na meko tkivo, kontinuirana adaptacija na intrizične i ekstrizične promjene (3).

1.1.3. Rast nazomaksilarnog kompleksa i mandibule

Rast nazomaksilarnog kompleksa odvija se kroz dva osnovna mehanizma: pasivna translokacija do koje dolazi zbog rasta kranijalne baze koja gura maksilu prema naprijed te aktivni rast maksilarnih struktura i nosa. Po rođenju prevladava rast na sinhondrozama kranijalne baze koji završava oko 7. godine zajedno s neuralnim rastom. U razdoblju od 7. do 15. godine oko trećine ukupnog pomaka maksile prema naprijed može se pripisati pasivnom premještanju, a ostatak je rezultat aktivnog rasta na maksilarnim suturama kao odgovor na podražaje okolnih mekih tkiva.

Najznačajniji medijatori rasta nazomaksilarnog kompleksa su hrskavica nosnog septuma i lakrimalna sutura.

Prema teoriji nazalnog septuma (7), za remodelaciju i anteriorni pomak nazomaksilarnog kompleksa velik utjecaj ima hrskavica nosa. Ona je specijalno adaptirano tkivo koje na pritisak odgovara manjim dijelom enhodralnom proliferacijom koja dovodi do linearnog rasta, a većim dijelom stvara fizičku silu koja nastaje ekspanzijom hrskavice i posljedičnog guranja maksile naprijed i dolje.

Maksila se sastoji od nekoliko funkcijskih cjelina koje su međusobno ovisne. Mjesto remodelacije je straga i gore što dovodi do translacije maksile naprijed i dolje. Jedan od medijatora koji sudjeluju u pomaku maksile prema dolje je lakrimalna sutura koja se nalazi uz suznu kost. Suzna kost je malena kost okružena drugim kostima u medijalnom dijelu orbite. Njezin suturalni sustav tijekom rasta omogućuje klizanje uz suture ostalih dodirnih kostiju.

Rast kosti uz mediosagitalnu suturu nepca sudjeluje u širenju nepca i alveolarnog luka i odvija se po principu slova „V“. Dno nosne šupljine pomiče se prema dolje zbog spuštanja nepčane ploče koja nastaje apozicijom s oralne strane i resorpcijom s nazalne strane.

Višestruki procesi apozicije i resorpcije na vanjskoj plohi maksile u velikoj su mjeri odgovorni na raznolikost ljudskog lica. Frontalni nastavak maksile i nosna kost rastu apozicijom prema naprijed. Nošen silama rasta kranijalne baze i spojišta dezmokranija i hondrokranija (zygomatico-frontalna i zygomatico-temporalna sutura) maksila i zigomatični luk premještaju se prema naprijed i dolje i postaju širi.

Tuber je najvažnije mjesto rasta posteriornog dijela maksile i jedno je od sekundarnih centara rasta koje se remodelira prema straga i natrag te tako pomiče maksilu i alveolarni nastavak

prema naprijed. Rastom tubera prema natrag povećava se duljina zubnih lukova što omogućuje nicanje trajnih kutnjaka.

Pomak maksile prema naprijed posljedica je i pozicioniranja i pomaka (translokacije) cijelog nasomaksilarnog kompleksa i prednje lubanjske baze koje nastaje kao posljedica rasta frontalnih i temporalnih režnjeva. Vertikalni rast maksile, uz translacijski pomak i suturalni rast, u velikoj je mjeri određen vertikalnim rastom alveolarnog nastavka i rastom zuba. Alveolarni greben sa zubima i nepčana ploča pomiču se prema dolje uslijed resorpcije s nazalne i apozicije s oralne strane. Njihov rast je posljedica kombinacije intenzivne remodelacije s relokacijom prema principu slova „V“, primarne te sekundarne translacije. Najintenzivniji vertikalni rast maksile odvija se u vremenu izmjene mliječnih u trajne zube pa je vertikalna dimenzija zadnja koja se formira tijekom procesa rasta (8).

Kao jedina pokretna kost lica, mandibula svojim specifičnim oblikom sudjeluje u različitim funkcijama: s temporomandibularnim zglobom je povezana sa srednjom lubanjskom jamom, alveolarni nastavci nose zube, za mandibulu se hvataju snažni žvačni mišići te njezin unutrašnji prostor ispunjava kompleksni mišićni sustav jezika.

Pri rođenju, mandibula je mala i njezin rast kasni u odnosu na rast ostalih komponenata kraniofacijalnog sustava. Ona ima kompenzatornu ulogu u uspostavi funkcije žvačnog sustava, gonijalni kut je otvoren, a pozicionirana je posteriorno kako bi dijete što lakše prošlo kroz porođajni kanal. Kasnije, tijekom rasta i razvoja, mijenjaju se odnosi korpusa i ramusa te odnosi maskile i mandibule međusobno. Intenzivan rast mozga (posebno frontalni i lateralnih režnjeva) povećava i pozicionira nazomaksilarni kompleks prema naprijed, dolje i lateralno. Ujedno se cijelo lice i mandibula rotiraju prema natrag, zbog toga je lice čovjeka ravnije nego kod primata. Rast mandibule slijedi gotovo u svim dimenzijama princip slova „V“ (procesi resorpcije dominantno se događaju s unutarnje strane, a apozicije s vanjske strane mandibule), tako se širina lica u donjoj trećini povećava horizontalno te se istovremeno povećava vertikalna dimenzija lica. Rast mandibule možemo promatrati kroz rast kondilarne hrskavice i rast ramusa. Bilo kakvo rano oštećenje kondilarne hrskavice dovodi do ozbiljne redukcije ukupnog rasta mandibule. Kondilarna hrskavica pripada sekundarnom tipu što znači da se ne razvija diferencijacijom primarno iz uspostavljenih hrskavica (Meckelova ili hrskavice kranijalne baze). Njezin sekundarni razvoj služi kako bi omogućila artikulaciju mandibule s kranijom i nije odlučujući centar rasta, već mjesto rasta mandibule (4).

Ramus je glavni centar mandibularnog rasta i njegova gornja stražnja strana je mjesto najintenzivnije aktivnosti. On kondil translatira prema gore, a mandibulu prema naprijed i dolje. Također ima važnu ulogu u postavljanju tijela mandibule i zubnog luka u odnosu na rastuću maksilu. Tijekom rasta uspravlja se iz dominantno horizontalnijeg položaja u vertikalniji, pa se mandibularni kut smanjuje. Nakon uspravljanja ramusa ponovo dolazi do promjene obrasca: donji dio prednje plohe ramusa se resorbira, a na prednjoj plohi gornjeg dijela odvija se apozicija. Ta resorpcija prednje plohe ramusa uz promjenu rotacijskog obrasca povećava prostor donjeg zubnog luka i omogućuje nicanje donjih kutnjaka. Zaključno, možemo reći da horizontalni, anteroposteriorni razvoj ramusa ovisi o razvoju farinksa te ektokranijalnog dijela medijalne endokranijalne fose - temporalni lobus mozga. Horizontalni razvoj dovodi mandibularni luk u okluziju s maksilarnim, slijedeći koncepte i obrasce rasta bazikranija. Vertikalni rast ramusa odvija se adaptacijom na vertikalni rast medijalne kranijalne fose (clivus), odnosno na vertikalnu ekspanziju nazalnog dijela respiratornog puta.

Rast ramusa u vertikali posljedica je enhondralne i periostalne aktivnosti kondilarne hrskavice. Na njezinoj površini događaju se hiperplazija, hipertrofija i enhondralna osifikacija. Sva druga područja manidbule formiraju se direktnom površinskom apozicijom i remodelacijom i tako se odvija horizontalni rast.

Intenzitet rasta mandibule prije puberteta relativno je stabilan i iznosi 1 do 2 mm godišnje povećanje visine ramusa i 2 do 3 mm godišnje produženje korpusa.

Zaključno, možemo reći da na konačan izgled i položaj mandibule utječe: ekspanzija medijalne i anteriorne kranijalne fose, erupcija zuba, rast farinksa, bilateralna asimetrija, povećanje jezika, usana, obraza, promjena mišićne aktivnosti, varijacije oblika glave, povećanje nazalnih puteva, obrazac gutanja, adenoidne vegetacije, pozicija glave za vrijeme spavanja, postura tijela te različite morfološke i funkcionalne varijacije (3).

1.1.4. Genetička i epigenetička kontrola kontrola rasta kraniofacijalnog sustava

Rast i razvoj kraniofacijalnog sustava čovjeka pod značajnom je kontrolom genetičkih čimbenika, odnosno pod utjecajem pojedinih skupina gena čija je aktivacija i ekspresija dobro programirana. Kontrolni genetički mehanizmi većim su dijelom nespecifičnog karaktera, poput regulacijskih gena koji ne djeluju samo na kraniofacijalni sustav, već na cijeli organizam. S druge strane, postoje vrlo specifični kontrolni obrasci razvoja koji uspostavljaju fizionomiju specifičnu za vrstu s relativno malim morfološkim varijacijama. Iako se čini da su varijacije čovječjeg lica velike, one su zapravo minimalne s obzirom na složenost razvojnog ciklusa (9).

Mjere većine tjelesnih proporcija, pa i simetrije lica, pod utjecajem su međudjelovanja većeg broja gena što nazivamo multifaktorsko ili poligensko nasljeđivanje. Takav naziv označava da ispoljavanje određenog svojstva ovisi o djelovanju više gena od kojih svaki pridonosi izraženosti s tzv. aditivnim učinkom. To znači da je za pojavu nekog svojstva ili bolesti potrebno djelovanje svih gena zajedno, pa se kaže da je utjecaj kumulativan jer niti jedan gen nije dominantan ili recesivan.

Od 25 000 ljudskih gena dvije trećine sudjeluju u kraniofacijalnom razvoju. Jedna od najvažnijih skupina gena uključena u embrionalni kraniofacijalni razvoj organizma su transkripcijski faktori koji kontroliraju transkripciju (prepisivanje) RNA s kalupa molekule DNA. Proteinski produkti ovih gena vežu se za regulacijske sljedove na molekuli DNA i stvaraju komplekse koji omogućuju transkripciju (prepisivanje) određenog gena. Transkripcijski faktori „uključuju“ i „isključuju“ gene, a njihova specifična struktura sastoji se od dviju domena: transkripcijska aktivna domena i DNA-vežuća domena koja može biti različitog oblika (uzvojnica-okret-uzvojnica, cinkovi prsti, leucinski zatvarač, uzvojnica-omča-uzvojnica). Geni koji kodiraju transkripcijske faktore organizirani su u genske porodice (**Tablica 1**.) (10).

Tablica 1. Genske porodice koje sudjeluju u kraniofacijalnom razvoju (preuzeto iz Stern C, 1973.) (10).

Hox	39 gena u 4 subporodice	kraniofacijalni razvoj za vrijeme embriogeneze
Dlx	DLX1, DLX2, DLX3, DLX4, DLX5, DLX6	kraniofacijalna morfogeneza i normalno formiranje čeljusti kod kralježaka
Msx	MSX1, MSX2, MSX2P1	kritični čimbenici uključeni u kraniofacijalni razvoj
Hand	HAND1 (5q33) i HAND2 (4q33)	razvoj škržnih lukova
Prrx	PRRX1 I PRRX2	eksprimacija maksilarnog i nazofrontalnog nastavka u kasnijim fazama razvoja
Fox	FOXO1B, FOXO3B	kranofacijalna morfogeneza
Pax	PAX3	formiranje kostiju lica i lubanje

Osim što geni mogu biti aktivni samostalno ili u genskim porodicama, njihovu ekspresiju mogu uvjetovati okolišni ili unutarnji, epigenetski te hormonalni ili enzimatski čimbenici (1). Koliki je odnos ukupne genotipske varijance u ukupnoj fenotipskoj varijanci, govori nam nasljednost. Ona se izražava brojkom, od 0 do 1. Vrijednost 0 pokazala bi da nema genetičkog utjecaja na neko fenotipsko svojstvo, dok bi vrijednost 1 značila da je svojstvo potpuno genetički određeno bez ikakvog utjecaja okolišnih čimbenika. Veći utjecaj okolišnih čimbenika i manji utjecaj nasljeđa smanjit će vrijednost nasljednosti. Ipak, za većinu svojstava nasljednost se kreće između 0,4 i 0,6. Kada je vrijednost iznad ili ispod ovog raspona, govori se o većem ili manjem utjecaju nasljeđa na razvijanje ili tzv. morfološku ili fiziološku ekspresiju pojedinog obilježja. Rezultati istraživanja pokazuju različite vrijednosti nasljednosti za isto svojstvo u različitim populacijama ili u istim populacijama, ali u različitim vremenskim periodima (11).

Epigenetička kontrola ispoljavanja gena proizlazi iz Wadingtonove hipoteze. Sve stanice našeg organizma potječu od jedne oplođene jajne stanice koja nakon razvoja organizma daje 200-tinjak različitih tipova stanica. Sve one i dalje imaju isti genom, ali su tijekom razvoja

pod utjecajem različitih faktora rasta, hormona i ostalih signalnih molekula postale diferencirane stanice različitih tkiva. Da bi postale različite, morale su drugačije pakirati svoj kromatin i tako omogućiti aktivnost različitih gena u različitim stanicama. Kromatin se pakira u područja koja su dostupna trankripcijskoj mašineriji (otvoreni ili eukromatin) i ona koja to nisu (zatvoreni ili heterokromatin). Razlika između tih dviju vrsta kromatina ostvarena je različitim informacijama koje stižu na istu DNA u različitim stanicama. Te se informacije upisuju „na“ ili „preko“ DNA, a nastali upis osnova je pojma „epi“genetika (12).

Budući da se genom ne smije mijenjati na zahtjeve niti stanice niti okoliša, već mora ostati nepromijenjen tijekom čitavog života stanice, on nije taj koji stanici može osigurati adaptibilnost na zahtjeve okruženja ili organizma. Kako stanica stalno komunicira s okolišem kao i s drugim stanicama istog organizma, tako prima informacije o potrebama organizma i zahtjevima okoliša. Epigenetor je element epigenetičkog puta koji nosi tu informaciju. On prenosi informaciju epigenetičkim inicijatorima koji određuju dijelove genoma čijom se reorganizacijom ekspresije omogućuje najbolji stanični odgovor, odnosno adaptacija na dobiveni zahtjev. Na krajnjem segmentu epigenetičkog puta nalaze se epigenetički održivači, elementi koji prevode zahtjeve epigenetičkih inicijatora u epigenom. Održivači također omogućuju molekularni mehanizam staničnog pamćenja koji se prenosi na stanice potomke staničnom diobom. Tako stanice kćeri unaprijed imaju određeni fenotip koji najbolje odgovara organizmu. Oni su dakle ti koji određuju status i funkciju kromatina bez zadiranja u DNA sekvencu, odnosno genom. Epigenetički put omogućuje rast, mirovanje stanice, proliferaciju, apoptozu, diferencijaciju te akomodaciju, a u promjene epigenetičkih faktora ubrajamo modifikaciju histona, metilaciju DNA te RNA modifikaciju (13).

Epigenetički lokalni čimbenici određeni su genetički, ali sudjeluju izvan stanica u kojima nastaju. Dijele se na opće i lokalne epigenetičke. Najpoznatiji primjer lokalnog epigenetičkog utjecaja je membranozna osteogeneza mandibule koja je dijelom modulirana Meckelovom hrskavicom - njezin način rada određen je unutarnjim genetičkim faktorima. Sljedeći primjer je baza lubanje čiji je rast uglavnom genetički predodređen i smatra se lokalnim epigenetičkim utjecajem koji utječe na razvoj drugih susjednih skeletnih struktura kao što su gornja i donja čeljust (12).

Prema epigenetičkoj hipotezi, i struktura i funkcija razvijaju se prema biokemijskim, biofizičkim, biomehaničkim i bioelektičnim parametrima razvoja organizma, intra i ekstracelularno, a okolina je ograničavajuća, regulativna i potpomažuća.

Saznanje da faktori okoliša, posebice prehrane, mogu promijeniti epigenom potomstva ukazuje na važnost upoznavanja epigenetičkih procesa za vrijeme rasta u razvoja i daje novi pogled na zdravu trudnoću. Kako se epigenetičko nasljeđivanje održava tijekom nekoliko generacija potomstva i nepromišljeni način života poput pušenja, fizičke neaktivnosti i neprilagođene prehrane naših djedova i baka određuje nas danas, jednako tako će i naš način života zasigurno odrediti kraniofacijalni fenotip i sklonost ili otpornost prema bolestima naših, u najmanju ruku, unuka (14).

1.1.5. Teorije kraniofacijalnog rasta

Od početka 20. stoljeća više autora usmjerilo je svoja istraživanja na kraniofacijalni rast. To je dovelo do progresivnog napretka brojnih, u to vrijeme sukobljenih, teorija o ovoj temi. Tijekom povijesti prevladavaju tri osnovna razdoblja. Prvi, dominantno do pedesetih godina prošlog stoljeća, kada prevladava genetička paradigma. Ona smatra kako je kraniofacijalni rast isključivo genetički određen i nepromjenjiv, suture su primarna mjesta rasta, rast se odvija periostalnom depozicijom i endosealnom resorpcijom, a hrskavice kranijalne baze, nazalnog septuma i kondila su primarni centri rasta. Genetičke teorije pripisuju glavnu ulogu genetici i negiraju mogućnost utjecaja susjednih tkiva i funkcionalnih čimbenika na morfogenezu. Od četrdesetih godina dvadesetoga stoljeća jačaju funkcionalističke teorije od kojih je dominantna Mossova teorija funkcijskog matriksa. Ona potpuno težište stavlja na funkcijske utjecaje u kraniofacijalnom rastu i smatra kako morfologija kosti nije genetički determinirana. Krajem stoljeća pojavljuju se revidirane funkcionalističke, ali i genetičke teorije koje se konačno stapaju u suvremene sintetske teorije kraniofacijalnog rasta.

1.1.5.1. Genetičke teorije

Genetičke teorije smatraju da je razvoj svih kranijalnih koštano-hrskavičnih elemenata kontroliran informacijama pohranjenim u genima. Hrskavica, periost i suture su pod kontrolom istih intrizičnih, osteogenetičkih kontrolnih mehanizama i predstavljaju autonomne centre rasta koji nisu pod utjecajem lokalnih faktora. Stoga genetičke teorije smatraju da se na kraniofacijalni rast ne može utjecati. Lice je stabilno u smjeru svog rasta; zubi i alveolarni nastavci su jedina područja na koje možemo utjecati i izazvati promjene (15).

Scottova teorija nazalnog septuma smatra kako je rast u trenutku rođenja reduciran samo na područje nosnog septuma koji djeluje na vomeralni sulkus i služi kao regulator rasta za gornji dio skeleta lica. Hrskavica nosa pretežito potiskuje primarno nepce prema dolje i u širinu te je zajedno s Meckelovom hrskavicom dominantna sila u formiranju lica (7). Prema Scottu, hrskavice i sinhondroze su centri rasta kontrolirani unutarnjim genetičkim faktorima. U suturama i sindezmozama, s druge strane, rast podliježe djelovanju lokalnih epigenetičkih i okolišnih čimbenika (15).

U početku života kosti se razvijaju vođene genetičkim čimbenicima, kasnije funkcionalni čimbenici igraju sve važniju ulogu u određivanju oblika i gustoće cjelokupnog kostura lica. Zapravo, kada kost nije u funkciji, sklona je atrofiji ili ne naraste do normalne veličine (7). Scottova teorija tvrdi da je periostalni rast upravljan genima pojedinca, dok Van Limborg i gotovo svi ostali autori vjeruju da je to područje rasta koji se sekundarno adaptira kao što je slučaj i sa suturama (16).

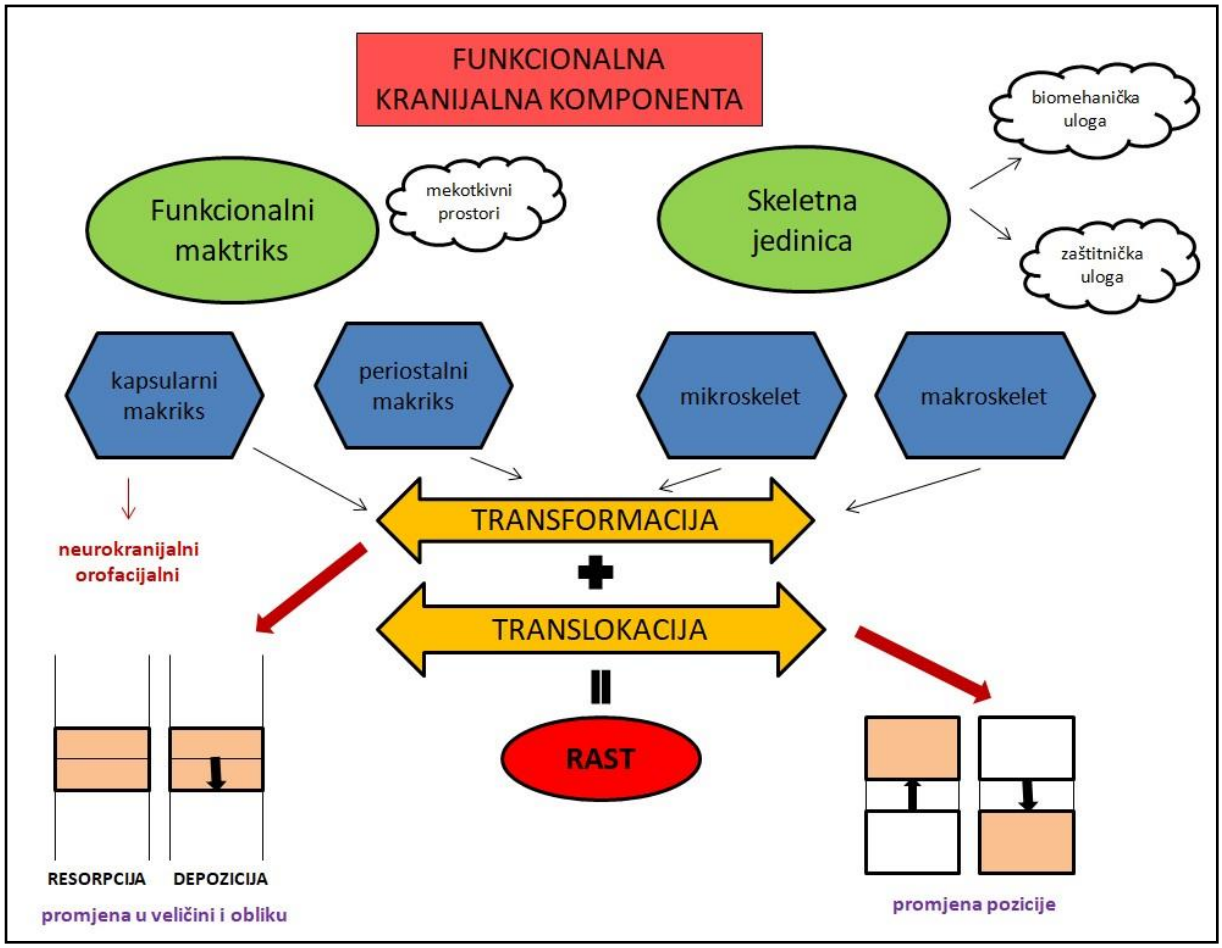
1.1.5.2. Teorija funkcijskog matriksa

Teorija funkcijskog matriksa (TFM) temelji se na postavci da u području glave postoji devet cjelina koje su međusobno neovisne (svod lubanje, baza lubanje, slušne kapsule, regija nosa, orbitalne šupljine, sustav potpore lica, usna šupljina, ždrijelo i mišići), a koje su odgovorne za pojedine funkcije (govor, sluh, vid, nju, probava, disanje, bazalne funkcije i neuralna integracija). Svaka od tih cjelina povezana je s koštanim sustavom lubanje i naziva se „funkcionalna kranijalna komponenta“ te se sastoji od djelatnog matriksa i skeletne jedinice. Uloga djelatnog matriksa je izravno izvršenje određene funkcije, dok je uloga skeletne jedinice biomehanička potpora i zaštita djelatnog matriksa (17).

Svaka skeletna jedinica, osim koštanog, obuhvaća hrkavično i vezivno tkivo. Ona se može sastojati od više mikroskeletnih jedinica sa svojim djelatnim matriksom. Tako je izgled kosti uzrokovan slijedom funkcionalnih zahtjeva djelatnih matriksa svake pojedine „mikro-skeletne jedinice“. Proučavanje morfoloških obilježja koštanih struktura glave stoga predstavlja indirektno proučavanje jedne ili više funkcija u kojima pojedino obilježje sudjeluje kao integralni dio mekih tkiva, a koje u konačnici i formira tu istu morfologiju (18).

Postoje dva oblika djelatnog matriksa (19) - periostalni i kapsularni matriks. Periostalni matriks djeluje na skeletnu jedinicu izazivajući na njoj morfološke promjene apozicijom i

resorpcijom koštanog tkiva pa se mijenja oblik i veličina skeletne jedinice. On ima središnji, lokalni učinak i obuhvaća različita tkiva kao što su mišići, krvne stanice, zubi ili živci. Stimulira rast skeletnih jedinica, direktno u skeletnom tkivu ili indirektno fuzijom s vanjskim fibroznim slojem periosta (2) (**Slika 1.**).



Slika 1. Uloge i djelovanja pojedinih komponenti teorije funkcijskog matriksa (autorsko djelo).

Kapsularni matriks sadrži i funkcionalne prostore, poput usnog, nosnog i ždrijelnog prostora koji mijenjaju položaj u prostoru određene skeletne jedinice (20). Takvi prostori nisu samo prazne šupljine, već integrirani negativni dio pojedine pozitivne cjeline u funkcionalnom skladu s djelatnim matriksom i skeletnom jedinicom (21). Najznačajniji primjer predstavlja neurokranijalni kapsularni matriks. To je ukupni volumen neuralne mase i kod ekspanzije neurokranijalne kapsule uvijek raste proporcionalno s povećanjem neuralne mase. Ekspanzija

neuralne mase uvijek je prvi događaj koja uzrokuje sekundaran, kompenzacijski rast lubanje. Orofacijalni kapsularni matriks predstavlja orofacijalni funkcionalni prostor okružen orofacijalnom kapsulom. Granica je koža izvana i mukozna membrana iznutra.

Mikroskeletne jedinice su dijelovi kosti čiji je rast moduliran periostalnim matricama (primjer temporalis - koronoidni nastavak, maseter - gonijalni kut). Rast se ovdje odvija isključivo transformacijom (intraoselani rast).

Makroskeletne jedinice su maksila, mandibula ili, primjerice, neurokranij. Ekspanzija kapsularnog matriksa uzrokuje pasivan položaj (promjenu) makroskeletne jedinice, tj. translacijski rast skeletne strukture.

Teorija funkcionalnog matriksa objašnjava kako sva skeletna tkiva imaju određeni stupanj savitljivosti tijekom rasta i razvoja. Kraniofacijalni kompleks je ontogenetički i filogenetički visoko adaptiran na funkcionalne zahtjeve i zahtjeve okoliša. Nasljednost i geni nemaju aktivnu ulogu u rastu. Mijenjanje, rast skeletnog tkiva i organa uvijek je sekundaran i obvezan odgovor na stalne događaje i procese koji se događaju u posebnim „neskeletnim tkivima“, organima ili funkcionalnim prostorima (funkcionalne matrice). Teorija ne objašnjava kako se neki aktualni morfogeni procesi događaju, već samo opisuje što se događa u kombinaciji akcije/reakcije i povratne informacije. Zbog toga je razumljivo da postoje određeni stavovi koji se suprostavljaju čisto funkcionalističkoj teoriji. Dvije su osnovne skupine stavova koji se suprostavljaju teoriji funkcijskog matriksa:

1. Metodologijska kritika koja kritizira TFM jer koristi samo mikroskopska mjerenja, samo specifične opcije bez objašnjenja strukturalnih detalja, samo kvalitativni, a ne kvantitativni opisi, tj. teorija nema kinetike i opisa dinamike rasta.

2. Hijerarhijska kritika tvrdi kako TFM ne objašnjava kako se ekstrizični, epigenetički i funkcionalni stimulusi transduciraju u regulatorne signale na celularnoj, multicelularnoj i molekularnoj razini (2).

1.1.5.3. Revidirana teorija funkcijskog matriksa

Upravo iz hijerarhijske kritike proizašle su promjene, TFM, odnosno revidirana teorija. Nova revidirana TFM pokušava biti most od genoma do organa preko dvaju koncepata: mehanotransdukcije i multicelularnog djelovanja stanica.

Mehanotrandukcija je proces kojim se mehanički stimulusi konvertiraju u biološki signal kako bi nastao celularni odgovor. Djelovanjem eksternih podražaja na stanicu preko mehano receptora događa se promjena signala u intracelularni signal što se naziva mehanotransdukcija. Mehanotransduktivnim se procesima periostalni funkcionalni stimulusi (ionski ili mehanički), prema ovoj teoriji, pretvaraju u skeletni celularni signal.

Među stanicama postoji dobro razgranati sustav poveznica, odnosno mreža pomoću koje se objašnjava intercelularna transmisija signala. Sve stanice kosti međusobno su povezane preko intercelularne mreže. Poveznica je međuplazmatski sustav sitnih kanala, tj. povezanost između osteona i intersticijskih regija (2).

Mehanotrandukcija aktivira koštane stanice tako što osteociti mogu inicirati početni membranski potencijal koji se pritom prenosi kroz connected cellular network (CNN). Ta poveznica je samoorganizirajuća, samoadaptirajuća i epigenetički regulirana, stabilan, ali dinamičan sistem sa stalnim promjenama preko sustava povratne sprege.

Biološka struktura je hijerarhijski organizirana sa strukturnom i funkcionalnom kompleksnošću koja se povećava počevši od subatomske razine do stanice, tkiva i organa. Uzročni, kontrolirani, regulirajući i determinirajući čimbenici koji utječu na biološke strukture mogu biti kategorizirani kao intrizični i ekstrizični. Intrizični se dalje klasificiraju kao „prioritetni“ uzroci koji utječu na nastanak prije nego se formira već specifična struktura. Oni utječu na vitalne funkcije unutar i među stanica te utječu na formu tkiva. Ekstrizični utječu na učinkovitost i djelotvornost razvoja i uglavnom predstavljaju epigenetičke mehanizme (2).

1.1.5.4. Suvremene teorije

Von Limborgova (kompromisna) teorija, sintetska teorija, servo sistem teorija Aleksandra Petrovića, Johnsovova limitirajuća teorija kotača te Voudourisova hipoteza relativnog rasta novijeg su datuma. Sve one do sada poznate i pretpostavljajuće mehanizme kombiniraju pokušavajući shvatiti i objasniti biologiju rasta i razvoja na mikro i makro nivou. Od navedenih teorija posebnu pažnju zaokuplja Von Limborgova (kompromisna) teorija koja uspijeva ujediniti današnja dominantna gledišta na mehanizme koji upravljaju procesima rasta i razvoja. Ona navodi kako u početku rasta i razvoja unutarnji (genetički) čimbenici imaju dominantnu ulogu u upravljanju složenim procesima. S protokom vremena, sve se više uključuju i lokalni, epigenetički, hormonalni, mišićni, funkcijski i okolišni čimbenici

prikazani u **Tablici 2**. koji utječu na smjer, intenzitet, vrijeme i dinamiku rasta. Uz koštane strukture sustavno rastu meka tkiva (mišići, vezivo, koža, osjetni organi). Oni svojim rastom i funkcijskim potrebama djeluju na sekundarne centre koštanog rasta pa tako u konačni izgled ugrađuju funkcijske zahtjeve mekih tkiva (22).

Tablica 2. Von Limborgova klasifikacija čimbenika koji utječu na kraniofacijalni rast (preuzeto iz Caprioglio A, 2001.) (22).

GENETIČKI	INTRIZIČNI GENETIČKI	utjecaj na razini stanice od kojih se tkivo sastoji (diferencijacija i stopa umnažanja)
	LOKALNI EPIGENETIČKI	lokalni utjecaj na stanice od kojih se tkivo sastoji
	GENERALNI EPIGENETIČKI	udaljeni utjecaj na stanice od kojih se tkivo sastoji
OKOLIŠNI	LOKALNI	ligamenti, tetive, mišići i ostala meka tkiva; zubi, funkcionalni prostor i ortognata sila
	GENERALNI	vaskularizacija, inervacija, prehrana, sistemske bolesti, oksigenacija, bolesti

Uzevši u obzir sve do sada objašnjeno, kontrola rasta može se objasniti kroz 12 sumacijskih točaka (6):

1. Rast je diferencijacijski proces progresivne maturacije. Različiti dijelovi imaju različit raspored razvoja. Različiti su vrijeme, brzina, regionalni iznos razvoja te različiti regionalni smjerovi. Tako, primjerice, vertikalni razvoj ima različito vrijeme morfogeneze od transverzalnog, a bilateralna bazikranijalna širina je naprednija u usporedbi s povećanjem zračnih facijalnih prostora i erupcije zuba. Bikondilarna i bizigomatična dimenzija korelira s ranom transverzalnom maturacijom temporalnog i frontalnog režnja. Rast ramusa adaptira se vertikalno na antero-posteriornu maturaciju faringealne komponente.
2. Razvoj je proces kojim se postiže ekvilibrijum, strikturalni i funkcionalni. Rast niti jednog dijela nije izoliran, već se stalno mijenja u veličini, obliki i odnosu između odvojenih dijelova i regionalnih komponenti svakog dijela.
3. Značajna je prilagodba pojedinih anatomskih dijelova i grupa dijelova: temporalni mišić i koronoidni nastavak, korijen zuba i alveola.
4. Ne postoji niti jedna centralna, kontrolna sila koja regulira razvoj svih kostiju.
5. Različiti tipovi tkiva su različitog kapaciteta za različite promjene za vrijeme rasta. Kost je na vrhu te piramide i ima veliku mogućnost adaptacije remodelacijom, dok je okluzijska ravnina pod jakim intrizičnim utjecajem.
6. Dva glavna pokreta za vrijeme rasta su remodelacija i pomak.
7. Varijacija oblika glave i lica (u širokom rasponu varijacija od dolihocefaličnih do brahicefaličnih tipova) nastaju zbog različitog bazikranijalnog obrasca facijalnog rasta. Oblik lica i proporcije su projekcija prednje kranijalne fose i tu je „korijen“ bazikranijalne asimetrije i posljedične asimetrije lica.
8. Dvonožna postura tijela, povećanje moždane mase i fleksura kranijalne baze utječu na inferoposteriornu rotaciju nazomaksilarnog kompleksa.
9. Rotacija maksile i/ili mandibule uvijek su kombinacija i pomaka i remodelacije i u podlozi je uvijek kompenzacijski mehanizam.
10. Regionalna adaptacija uvijek je dio kontrolnih mehanizama rasta i preslika je međusobnih dijelova. Primjer je visina ramusa koja je povezana s faringealnim prostorom i funkcionalnom pozicijom donjeg luka te u ovisnosti s gornjim lukom.

11. Kliničkom intervencijom se na procese rasta može djelovati kao klinički inducirani intrizični kontrolni signali koji, dok djeluju, mogu usmjeravati rast i razvoj.
12. Smjer mimične i facijalne muskulature suprotan je od smjera rasta obiju čeljusti. Povećanje masetera i temporalisa utječe na konačan položaj mandibule.

U svakoj od navedenih sumacijskih točaka kraniofacijalnog rasta možemo očekivati različite poremećaje ili nepravilnosti koji će utjecati na nastanak širokog spektra kraniofacijalnih varijacija. Budući da ne postoji jednoznačan obrazac koji bi doveo do uniformnog fenotipa, svaka od prije navedenih 12 točaka kraniofacijalnog rasta i razvoja u sebi sadrži mogućnost nesimetričnog razvoja i nastanka različitih oblika asimetrije.

1.2. Utjecaj spolnog dimorfizma i hormonalnog statusa i procesa starenja na oblik kraniofacijalnog skeleta

Kao što je u prthodnom poglavlju navedeno, različiti dijelovi lica imaju različit razvoj u smislu vremena, brzine te smjera rasta i razvoja (6). Na trajanje tih procesa, kao i na promjene lica tijekom čitavog života, u velikoj mjeri značajnu ulogu imaju različita hormonalna međudjelovanja te vrijeme djelovanja i koncentracije pojedinih hormona koji, svaki sa svojim cjelovitim ili aditivnim učinkom, pridonosi promjeni morfoloških karakteristika lica.

Hormonalni status stoga predstavlja značajan čimbenik koji treba uzeti u obzir pri analizama morfoloških promjena kraniofacijalnog skeleta. Spolni dimorfizam jedan je od osnovnih funkcijsko-morfoloških obilježja prema kojem se razdvaja promatrana populacija i to upravo zbog jasnog razgraničenja i jasne različitosti djelovanja pojedinih hormona. Poznato je da testosteron čini robusniju formu jagodica, naglašene supraorbitalne lukove, snažniju čeljust i općenito izražajniju donju trećinu lica, dok estrogen čini gracilniji izgled nosa, očiju i jagodica. Na osnovu ravnoteže ili dominacije muških ili ženskih hormona, lice tijekom razvoja poprima obilježja koje mu daju karakteristike muškog ili ženskog lica (23). Uslijed pojačanog izlučivanja spolnih hormona u pubertetu dolazi do većih i bržih promjena u izgledu lica te se naglašavaju spolne različitosti. Dok kod oba spola u djetinjstvu prevladavaju ženske fenotipske karakteristike lica, nakon puberteta se formira spolni dimorfizam u svojoj punini. Potom se kod žena koštane promjene lica usporavaju nakon puberteta, dok se kod muškaraca topografske i dimenzionalne promjene nastavljaju tijekom kasnog adolescentnog perioda (23).

Muška lica su u prosjeku duža, šire čeljusti te naglašenijih supraorbitalnih lukova (tzv. arkade ili čeoni lukovi), dok su ženska lica manje čeljusti, punijih usana, manje izraženih čeonih lukova i izraženijih očiju (24). Žensko lice je ravnije i prema proporcijama čini se šire i općenito nježnije. Anatomske strukture lica koje imaju najizražajniji spolni dimorfizam su supraorbitalni brid i lukovi, glabelarna regija i trigonum mentale (25, 26, 27). Kako je nazalna regija dio dišnog sustava, postoji određena usklađenost veličina tako da nosna šupljina ima veće dimenzije kod muškarca nego kod žena. Stoga su i dimenzije vanjskog nosa veće kod muškarca. Muško je čelo više zakošeno, dok je kod žena ono uspravnije i zaobljeno. Uslijed izraženijeg i izbočenijeg nosa kod muškarca, dio čela uz korijen nosa također je izbočen. Mišićna hvatišta su bolje izražena kod muške nego kod ženske lubanje pa je to na licu vidljivo u području ruba hvatišta sljepoočnog mišića (*m. temporalis*). Orbite su kod muške lubanje manje i četvrtastije, zaobljenih rubova i jače izraženih supraorbitalnih lukova, dok su kod ženske lubanje orbite veće i okruglog oblika, oštrijih rubova i slabije izraženih supraorbitalnih lukova (28, 23).

Razvijenost brade vrlo je raširen znak dominantnosti i češći je kod muškog lica. Naglašenost mandibularnog kuta i mišića masetera licu daje dominantno muževnu karakteristiku, dok naglašenost jagodica, odnosno zigomatične regije lice feminizira. Mandibula ima spolno različite karakteristike jer je kod muškarca ona veća i šira, oštrijeg gonijalnog kuta, a brada četvrtastija i jače izražena dok je ženska mandibula manja i uža, s tupljim gonijalnim kutom i nježnijom i užom bradom (28, 23).

Ove karakteristike navedene su kao općenita obilježja za pojedini spol, no dinamika hormonalnog međudjelovanja rezultira preklapanjem i spajanjem spolno dominantnih karakteristika kao i njihovu promjenu tijekom vremena. To je posebice izraženo početkom perioda starenja koji je prirodan i ireverzibilan fiziološki proces koji podrazumijeva morfološke i fiziološke regresivne promjene. Danas je iz literature poznato mnogo različitih teorija kojima se pokušavaju opisati uzroci i mehanizmi starenja u organizmu, od trošenja, korištenja i zlouporabe tkiva, do smanjenog lučenja hormona, gomilanja slobodnih radikala u tkivima i sl., a čija je posljedica smanjena mogućnost obnove tkiva. Sve teorije imaju zajednički zaključak: posljedice starenja nisu jednake kod svih te ovise o genetskim čimbenicima te čimbenicima utjecaja okoline (29). Na razini organizma starenje se manifestira kao ukupan pad u funkcionalnom kapacitetu različitih organa da održe osnovnu homeostazu tkiva i da daju fiziološki primjeren odgovor na stres. Ovaj pad je postepen i

umjeren u srednjim godinama, no ubrzava se u starijoj dobi i postaje posebno vidljiv pod uvjetima koji izazivaju organizam da odgovori na različite stresore robusnim fiziološkim i/ili regenerativnim odgovorom (30).

Prve promjene lica mogu se uočiti u dobi između dvadesete i tridesete godine života (31). Pokazalo se da se koštana tkiva duž orbitalnog ruba, posebno superomedijalno i inferolateralno, resorbiraju s porastom dobi, dok središnji orbitalni dijelovi ostaju relativno stabilni tijekom cijelog života (32). Povlačenje koštane sredine i maksile u starijoj dobi pridonosi izgradnji i produbljivanju nazolabijalnih nabora i povećanju plosnatosti lica (33). Povećanje nosa rezultat je povećanja piriformnog otvora, dok se koštani rubovi povlače, osobito u procesu podizanja gornje čeljusti. Visina i dužina mandibule smanjuju se u starijoj dobi, dok se mandibularni kut povećava (34).

Bogin i suradnici (2018) ažurirali su Boginov sustav klasifikacije životnih stadija čovjeka. Ovi stadiji uključuju: primarni period odrasle dobi (18/20 - 35 godina), sekundarni period odrasle dobi (35 - 50 godina), prijelaznu, odnosno degeneracijsku dob (> 50 godina do starenja) i starost (varijabilni početak i napredovanje kao funkcija prethodne razine somatskih i kognitivnih rezervi) (35). Kako navodi Škarić-Jurić T., s obzirom da je starenje kontinuirani proces, dob prekretnice pri kojoj će se smatrati da netko pripada skupini osoba starije dobi, društveno je uvjetovana i ona se u današnjem trenutku u razvijenim državama svijeta obično pozicionira na dob oko navršene 65. godine života (30).

Istraživanja lica ukazuju da se dobna granica ne treba smatrati samo društvenom kategorijom, već ona ima svoje biološke temelje. Recentni rad na istoj populaciji na kojoj je provedeno i ovo istraživanje ukazao je kako kod ženske populacije već ranije, početkom menstrualne pauze, dolazi do značajnih promjena u morfološkim karakteristikama lica. Istraživanje naše znanstvene grupe pokazalo je da je stopa starenja lica kod žena (prosječan iznos - za razliku od promjene oblika u godini) veća od stope kod muškaraca. Prije dobi od 50 godina i nakon 60. godine, ženska lica u prosjeku stare dvaput brže od muških lica; između 50 i 60 godina ova razlika u stopi starenja još je izraženija (i do tri puta brža). Također, ova istraživanja ukazuju da nakon menopauze kronološka dob više nije dovoljna za dovoljno precizno predviđanje oblika lica, već je za to primjerenija tzv. menopauzalna dob (odnosno vrijeme od posljednje menstruacije).

Nakon menopauze žene pokazuju jače smanjenje u području čeljusti, osobito u području brade u usporedbi s muškarcima. Ta razlika među spolovima vjerojatno proizlazi iz različitih

hormonalnih promjena tijekom menopauze i andropauze kojima dominira smanjenje estrogena kod žena i smanjenje testosterona kod muškaraca. Poznato je da oba hormona utječu na metabolizam kostiju, ali resorpcija kosti prvenstveno kontrolira estrogen kod oba spola (36, 37, 38). Gubitak estrogena utječe i na kosti čeljusti (39, 40). Mnogo veća redukcija estrogena kod žena u odnosu na muškarce stoga može uzrokovati izraženiju resorpciju kosti kod žena (41). Zaključno, rezultati istraživanja tkiva lica pokazuju da su promjene morfologije lica značajno veće kod ženskog u odnosu na muški spol i da u najvećoj mjeri započinju u periodu kada počinje period menopauze, odnosno andropauze (42).

1.3. Asimetrija lica i razvojna nestabilnost

Asimetrija je odstupanje od identičnog oblika ili veličine dviju strana tijela. Postoji nekoliko klasifikacija asimetrije lica. Hendersonova klasifikacija asimetrije (4) je najopsežnija morfološka klasifikacija koja dijeli facijalnu asimetriju na: asimetrija donje, srednje i gornje trećine lica i rascjep usne i/ili nepca. Klinički najobuhvatnija je klasifikacija Bishare (2) koji je podijelio asimetriju prema etiologiji na: dentalnu, skeletnu, mišićnu i funkcionalnu. Asimetrija je jedna od najčešćih facijalnih karakteristika i preklapanje maksilarne i mandibularne središnje linije važni su ciljevi svake ortodontske terapije. Simetrija poboljšava estetiku zuba i lica, ali i funkciju i stabilnost konačnih ortodontskih rezultata.

Sve metode detekcije asimetrije (uključujući funkcionalnu i frontalnu analizu te radiološku metodu lokalizacije asimetrije) imaju isti nedostatak definiranja referentne medio-sagitalne ravnine. Umjesto nepreciznih mjerenja udaljenosti od te ravnine, modeliranje zrcalnog objekta može pružiti točniju procjenu kraniofacijalne asimetrije. Za modeliranje je važan pravilan odabir i digitalizacija dvodimenzionalnih i/ili trodimenzionalnih antropometrijskih (kefalometrijskih) točaka lica jer odstupanje simetrije ponekad može biti vrlo malo. Homologija, ponovljivost i dobra vidljivost točke na promatranoj anatomskoj strukturi važne su predispozicije za njihovu uporabu. Metoda objekta zrcaljenja klinički je i znanstveno primjenjiva za procjenu različitih tipova asimetrije (43).

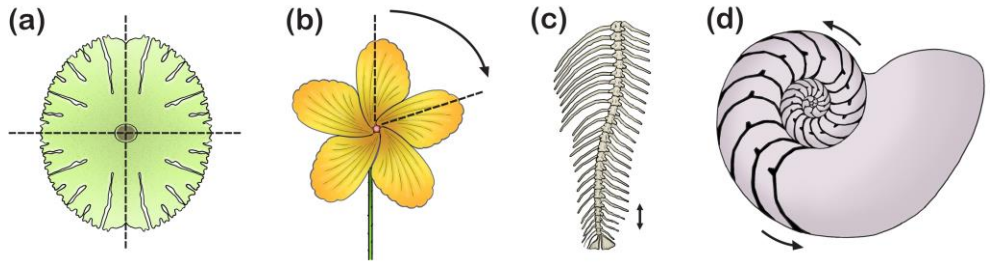
1.3.1. Vrste simetrije

Prije razmatranja asimetrije, korisno je osvrnuti se na simetriju jer je asimetrija odstupanje od simetrije. Simetrija bioloških struktura može se definirati kao ponavljanje dijelova u različitim položajima i orijentacijama. Takva simetrija je temeljna tjelesna značajka većine organizama i mnogih njihovih dijelova. Većina životinja je bilateralno simetrična, s lijevim i desnim stranama koje su jedna od druge zrcalne slike. Bilateralna simetrija, međutim, nije jedini tip simetrije u biološkim strukturama. Bilje, naročito, pokazuje širok raspon različitih vrsta simetrija u cvjetovima i drugim organima (44, 45, 46, 47).

Budući da je simetrija morfoloških struktura ponavljanje dijelova u različitim položajima i orijentacijama, korisno je uzeti u obzir broj i raspored ponovljenih dijelova kao način razumijevanja različitih tipova simetrije. Na primjer, poznata bilateralna simetrija većine životinja povezana je s ponavljanjem dijelova kao parova koji se nalaze na lijevoj i desnoj strani kao zrcalne slike jednih drugih. Za svaki par dijelova, odraz oko središnje ravnine preslikava lijevi dio na desni dio i obrnuto. Stoga je ta refleksija o središnjoj ravnini jako važna za bilateralnu simetriju i može se koristiti za njezinu karakterizaciju.

Ostale vrste asimetrije temelje se na različitim rasporedima dijelova (**Slika 2.**). Budući da su ti tipovi simetrije obično složeniji od bilateralne simetrije jer većina uključuje više od dva dijela, oni su podvrgnuti krovnom pojmu „složena simetrija“ - bilo koji tip simetrije osim bilateralne simetrije. Ovaj je izraz koristan jer strukture sa složenom simetrijom zahtijevaju posebne metode za morfometrijsku analizu (48) koje su generalizacija jednostavnijih metoda koje se rutinski koriste za bilateralnu simetriju (49, 50, 51).

Refleksija nije važna samo za bilateralnu simetriju, već se javlja i u različitim tipovima složene simetrije. Disimetrijska ili biradijalna simetrija, gdje postoje dvije okomite osi ili ravnine simetrije, još je jedan tip simetrije koji je rasprostranjen npr. u jednoćelijskim algama (**Slika 2a**.) (52, 53, 54) ili u mnogim cvjetovima (55, 56, 57, 58, 59). Dvije osi simetrije mogu biti različite u razvojnim i funkcionalnim aspektima (lijeva-desna os u odnosu na dorzalno-ventralnu ili adaksijalno-abaksijalne osi) što može biti od posebnog interesa (53, 54, 57).



Slika 2. Neke vrste složene simetrije: (a) simetrija refleksije s dvije osi simetrije (Micrasterias rotata, jednostanična alga); (b) rotacijska simetriju cvijeta; (c) translacijska simetrija (serijska homologija) kralješaka u kralježnici ribe; (d) spiralna simetrija komora nautilus ljuske (autorsko djelo).

Rotacija je također uključena u mnoge simetrije, bilo samostalno (**Slika 2b.**) ili u kombinaciji s refleksijom, tako da je svaki dio zrcalno simetričan kao u poznatoj radijalnoj simetriji mnogih cvjetova ili kod nekih beskralježnjaka kao što su morski ježevi i meduze. Svaka rotacija ima središte ili os i svaka rotacija ima redoslijed, broj ponavljanja dijelova koji su raspoređeni oko punog kruga (npr. **Slika 2b.** prikazuje rotaciju reda 5 ili 72°).

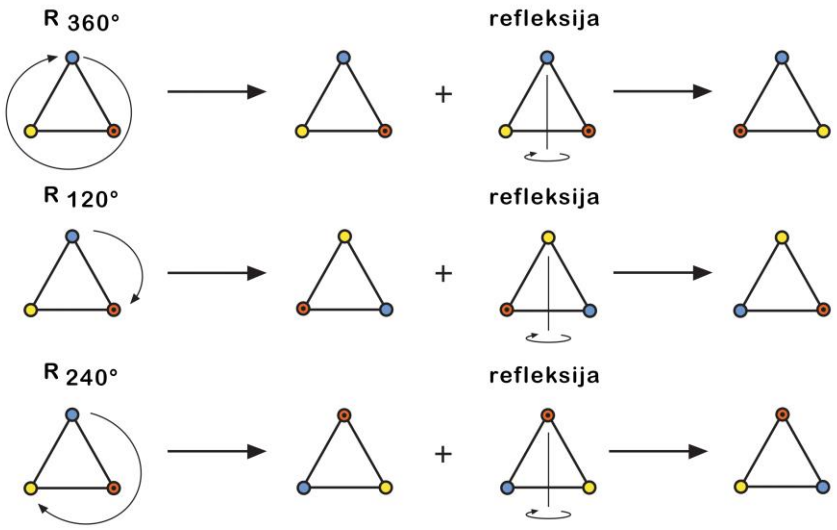
Daljnje moguće rješenje je ponavljanje dijelova uzduž osi, s translacijom kao promjenom između ponovljenih dijelova. Takva translacijska simetrija biolozima je možda više poznata pod nazivom serijska homologija. Pojavljuje se široko u tjelesnim planovima mnogih životinja koje pokazuju segmentaciju u nekom obliku (npr. kraljšci kralježnjaka, **Slika 2c.**) i također u mnogim biljkama gdje se lišće i drugi organi ponavljaju duž izbojaka. U tim primjerima translacija se često kombinira s rotacijom ili refleksijom.

Spiralna simetrija, gdje se rotacija i translacija odvijaju zajedno s ekspanzijom, drugi je tip simetrije koji se često vidi u morfološkim strukturama (npr. školjke puževa i drugih mekušaca, **Slika 2d.**). Ovi primjeri nisu nabrajanja mnogih simetrija koje se nalaze u morfološkim strukturama, već predstavljaju najraširenije tipove i stoga su korisne kao pregled najvažnijih tipova simetrije.

1.3.2. Simetrija matematički

Postoji opsežna i moćna matematička teorija o simetriji (60, 61, 62, 63) koja je ključna za razumijevanje složenih simetrija. Transformacije igraju važnu ulogu u ovoj teoriji. Transformacija mapira svaku točku objekta na neku točku u ravnini ili prostoru objekta i reverzibilna je. Transformacije s posebnim interesom za simetriju su: refleksija, rotacija i translacija koji definiraju raspored ponovljenih dijelova u simetričnoj strukturi (**Slika 3**.). Također, daljnja transformacija koja je vrlo važna je identitet, transformacija koja ostavlja svaku točku nepromijenjenom (može se također opisati kao rotacija za 360 ° ili kao rezultat dviju refleksija oko iste osi ili ravnine).

Objekt je simetričan ako transformacija ostavlja objekt nepromijenjenim. Transformacije koje ostavljaju objekt nepromijenjenim nazivaju se njegovim transformacijama simetrije. Simetrija objekta može se karakterizirati skupom svih njegovih transformacija simetrije. To je skup s nekim posebnim svojstvima koji se naziva grupa i stoga se naziva skupina simetrije. Svaka vrsta simetrije ima svoju karakterističnu skupinu simetrija (60, 61, 62, 63). Skupine simetrije mogu npr. kombinirati rotacije i refleksije. Primjer je skupine simetrije jednakostranični trokut (**Slika 3.**). U ovom slučaju, rotacija je reda 3 ili 120 ° što znači da grupa simetrije uključuje i rotacije za 240 ° i za 360 ° (ili 0 °, identitet opet). Svaka od tih rotacija može se dalje kombinirati s refleksijom (Slika 3; to mijenja jesu li uglovi trokuta označeni u smjeru kazaljke na satu ili suprotno od kazaljke na satu). Budući da se svaka rotacija može dogoditi s ili bez refleksije, skupina simetrije uključuje ukupno šest transformacija (**Slika 3**).

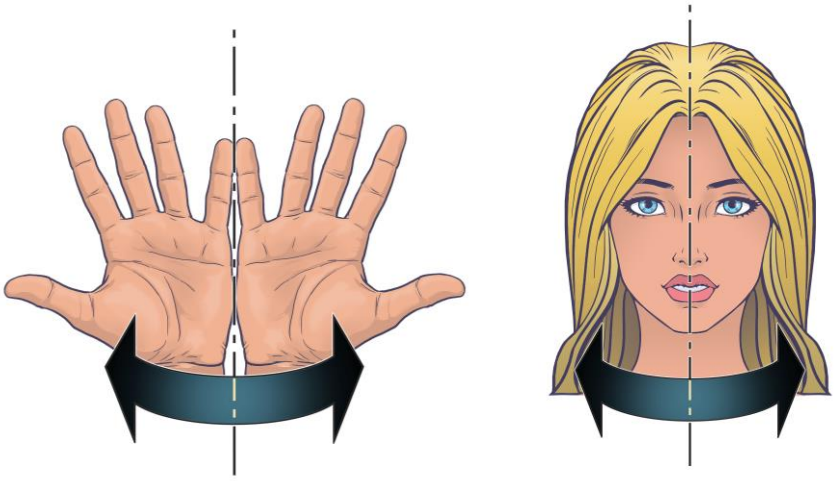


Slika 3. Skupina simetrije jednakostraničnog trokuta. Postoji šest simetrijskih transformacija u skupini simetrije: rotacije za 120 °, za 240 ° i za 360 ° (ili za 0 ° što je identitet), svaka s ili bez refleksije (autosko djelo).

Sve skupine simetrija nemaju konačan broj transformacija, postoji samo određeni skup transformacija simetrije, a kombiniranje tih transformacija na bilo koji zamisliv način uvijek donosi transformacije koje su već uključene u taj skup. Na **Slici 3c.** je translacijska simetrija kralježnice gdje se moguće transformacije kreću naprijed za jedan pršljen ili se kreću unatrag za jedan pršljen. Ako opetovano primijenimo jedan od njih, nikada se nećemo vratiti na istu transformaciju jer uvijek možemo dodati još jedan korak, a zatim još jedan i drugi. Naravno, u konačnici, ponestajat će nam kralježnice na prednjem ili stražnjem kraju, ali to nam samo govori da kralježnica kao cjelina nije stvarno simetrična pod translacijama. Skupine simetrije s translacijom sadrže beskonačan broj transformacija simetrije. Isto vrijedi i za spiralnu simetriju: u nautilusu (**Slika 3d.**) moguće je započeti u sredini i zatim korak po spirali ljuske iz komore u komoru, ali taj slijed nikada ne prestaje jer se uvijek može ponoviti nekoliko puta. Razlika između tih konačnih i beskonačnih skupina simetrije važna je za morfometrijske studije zbog određivanja koje se vrste analiza mogu koristiti za različite tipove simetrije.

1.3.3. Podudarna simetrija i simetrija objekta

Za analizu asimetrije oblika korisno je napraviti daljnju razliku između dviju vrsti simetrija ili, bolje rečeno, između dviju perspektiva simetrije. Prvo, postoji tip simetrije gdje je struktura prisutna kao dvije odvojene kopije, jedna na svakoj strani tijela, koje su zrcalne slike jedna druge. Poznati primjeri ove vrste simetrije su ljudske ruke ili krila insekata (**Slika 4a.**). Osovina ili ravnina simetrije prolazi između dviju kopija, ali nije dio ni jedne kopije. Kao rezultat toga, raspored dvaju dijelova u odnosu jednog na drugi nije aspekt njihove simetrije. Ovaj tip simetrije naziva se podudarna simetrija (50, 51) jer se lijeva i desna kopija mogu pomicati i međusobno uskladiti, na primjer stavljanjem dlanova lijeve i desne ruke zajedno.



Slika 4. Podudarajuća simetrija i simetrija objekta. (a) Podudarajuća simetrija. Postoje dva odvojena primjerka krila mušice, a os simetrije prolazi između njih; (b) Objektna simetrija. Lice je simetrično samo po sebi, a kroz njega prolazi os simetrije (autorsko djelo).

Alternativa je objektna simetrija gdje je predmet interesa simetričan sam po sebi (50, 51). Na primjer, ljudsko lice je simetrično jer su njegove lijeve i desne polovice zrcalne slike jedna od druge (**Slika 4b.**). Za strukture s objektnom simetrijom, os ili ravnina simetrije prolazi kroz strukturu. Stoga je relativni raspored dviju polovica integralni aspekt simetrije cijele konstrukcije.

Ova razlika ima važne implikacije za analize asimetrije. Za podudarnu simetriju, mogućnost podudaranja lijeve i desne kopije također nudi izravnu metodu za karakteriziranje asimetrije. Ako se zajedno pokuša uskladiti lijevu i desnu kopiju (kao lijevi i desni dlan ruke) što je više moguće, preostale razlike nastaju zbog asimetrije. Za objektnu simetriju situacija je nešto složenija jer se lijeva i desna polovica moraju uspoređivati kao dio cjelokupne strukture. Metoda analize simetrije objekta koristi superimpoziciju izvorne i kopiju zrcalne slike objekta za karakterizaciju simetrije i asimetrije. Objektna simetrija važna je za morfometrijske studije, čak i ako asimetrija nije u središtu interesa jer su lijeva i desna polovica strukture međusobno ovisne što potencijalno može uzrokovati probleme za analize (64). Za strukture s objektnom simetrijom istraživači stoga uvijek trebaju koristiti metode koje uzimaju u obzir simetriju (50, 51).

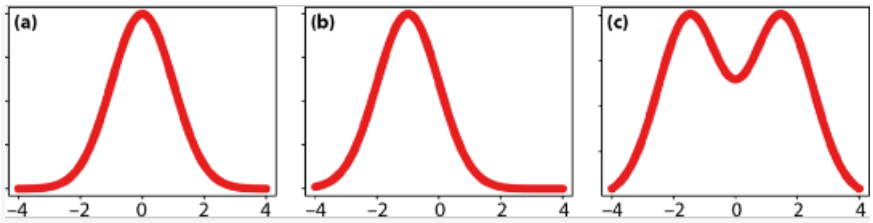
Razlikovanje podudarne simetrije i simetrije objekata lako je u većini slučajeva. Ključno je pitanje prolazi li medijana osi ili ravnina između lijeve i desne polovice tako da ih ostavlja slobodnim da se kreću u međusobnom odnosu ili prolazi kroz strukturu tako da su dvije polovice čvrsto povezane. Obično je ovo pitanje lako odgovoriti i stoga je jasno koja se vrsta analize treba koristiti (65).

Razlika između podudarne i simetrije objekata posebno je važna za tretiranje razlika u veličini između lijeve i desne strane. Za usporedbu simetrije, razlika u veličini lijeve i desne kopije dovodi do asimetrije za veličinu centroida, ali ona nema nužnu implikaciju za asimetriju oblika, osim ako se to ne dogodi. Asimetrije veličine i oblika dva su logički odvojena pitanja koja se mogu rješavati u odvojenim analizama. Nasuprot tome, za strukture s objektnom simetrijom, razlika u veličini između lijeve i desne polovice je aspekt oblika cijele strukture (npr. da je jedna polovica lica na Slici Zb manja od druge, ova će razlika biti obilježje oblika cijelog lica). Za objektnu simetriju, jer se cjelokupna konfiguracija razmatra kao cjelina, a ne kao dvije odvojene polovice, sve asimetrije između lijeve i desne polovice aspekti su oblika cjelokupne konfiguracije (51). Iz tog razloga, studije asimetrije u strukturama s podudarnom simetrijom obično provode odvojene analize asimetrije za veličinu centroida i za oblik, dok studije u strukturama s objektnom simetrijom provode analize asimetrije samo za oblik. Te analize služe kako bi se efekt veličine objekta maknuo iz analize asimetrije i kako na njega ne bi utjecao. To se radi tako da svi oblici svedu na jednu, prosječnu veličinu objekta koja se zove Prokrustova (48).

1.3.4. Distribucija asimetrije

Tradicionalno se razlikuju tri vrste asimetrije prema raspodjeli lijevo-desnih razlika u populaciji: direkcijska asimetrija, fluktuirajuća asimetrija i antisimetrija (**Slika 5.)** (66, 67).

Pojam antisimetrije označava razliku između lijeve i desne strane koja nastaje kao rezultat kompetitivnih mehanizama i interakcija (npr. ljevaci i dešnjaci). Pojam direkcijske asimetrije označava normalnu asimetriju kada je jedna strana bolje razvijena od druge i izražava se na razini populacije. Pojam fluktuacijska asimetrija predstavlja razliku unutar populacije, odnosno razliku između dvije strane iste jedinke koja nastaje uslijed nejednakog tijeka razvojnog procesa. Van Valen, za kojeg se smatra da je postavio temelje modernih analiza asimetrije (66), izjavio je da ove tri vrste asimetrije nisu međusobno isključive kategorije i da se mogu pojaviti zajedno, u istom svojstvu.



Slika 5. Frekvencijske raspodjele lijevo-desnih razlika tipičnih za tri glavne vrste asimetrije. a) „Čista“ fluktuacijska asimetrija: lijevo-desna razlika slijedi zvonoliku raspodjelu sa srednjom vrijednošću nula (nema direkcijske asimetrije); b) Direkcijska i fluktuirajuća asimetrija: lijevo-desne razlike raspoređene su oko srednje vrijednosti koja je različita od nule što ukazuje na direkcijsku asimetriju. Rasipanje pojedinih lijevo-desnih razlika oko te vrijednosti je fluktuirajuća asimetrija: c) Antisimetrija: raspodjela lijevo-desnih razlika je bimodalna što ukazuje na to je većina pojedinaca asimetrična, ali može biti pristana s lijeve ili desne strane (preuzeto iz Van Valen L, 1962.) (66).

Direkcijska asimetrija, fluktuirajuća asimetrija i antisimetrija vidljivi su obrasci u distribuciji lijevo-desnih razlika u populacijama organizama. Vrste asimetrije imaju različita statistička svojstva kao i različita biološka podrijetla i implikacije.

Također je vrijedno zapamtiti da su ovi obrasci asimetrije vidljive manifestacije bioloških procesa, ali da nisu sami procesi. Zaključak iz obrazaca asimetrije za biološke procese vrlo je ograničen i obično zahtijeva dodatne dokaze.

Fluktuacijska asimetrija je slučajna razlika između dvije strane za određeno svojstvo kod iste individue pa je karakterizirana slučajnom distribucijom. Iznos fluktuacijske asimetrije unutar cijele populacije kreće se oko nule. Ona nije nasljedna (68), ali nasljeđe ima značajnu ulogu u njenom nastanku i razvoju.

Direkcijska ili međugrupna asimetrija je razlika između grupe koja predstavlja promatrani objekt i grupe koja opisuje srednju vrijednost (suma kvadrata razlike objekta u odnosu na srednju vrijednost). Ta razlika može biti različito velika, ali se prosječna razlikuje od nule. Najčešći primjer direkcijske asimetrije je raspored unutarnjih organa kod većine životinja i ljudi gdje je srce na lijevoj strani, crijevo namotano na konstantan asimetričan način, dok su drugi organi, pluća ili jetra također dosljedno asimetrična. Situs inversus - zrcalni raspored svih unutarnjih organa ili situs ambigus - zrcalni rapored samo nekih unutarnjih organa rijetki su poremećaji koji se smatraju ozbiljnim malformacijama i uzrokuju veliki morbiditet pogođenih osoba (69). Još od pojave geometrijskih metoda 1990-ih statistički značajna direkcijska asimetrija pronađena je praktički u svakom ranom istraživanju asimetrije oblika (70, 71, 72) i prepoznata kao stvarna i vjerojatno rasprostranjena pojava (49).

Antisimetrija je uzorak asimetrije gdje je većina pojedinaca asimetrična, ali se razlikuju u smjerovima asimetrija tako da postoji mješavina „lijeve i desne strane“ pojedinaca. Kao rezultat ove mješavine, distribucija lijevo-desnih razlika može biti bimodalna (**Slika 5c**.). Slabiji slučajevi antisimetrije, s manjim asimetrijama, možda neće proizvesti jasno bimodalnu distribuciju. Doista, čini se razumnim predvidjeti postupni prijelaz između antisimetrije i fluktuirajuće asimetrije. Nekoliko autora ističe da antisimetrija zahtijeva neku vrstu negativne korelacije ili povratne sprege između vrijednosti osobina na lijevoj i desnoj strani (66, 73, 74), dok ne postoji takva korelacija za fluktuirajuću asimetriju. Kontinuirani prijelaz između antisimetrije i fluktuirajuće asimetrije stoga se može promatrati kao da odgovara postepenoj promjeni od jake negativne korelacije prema korelaciji nule.

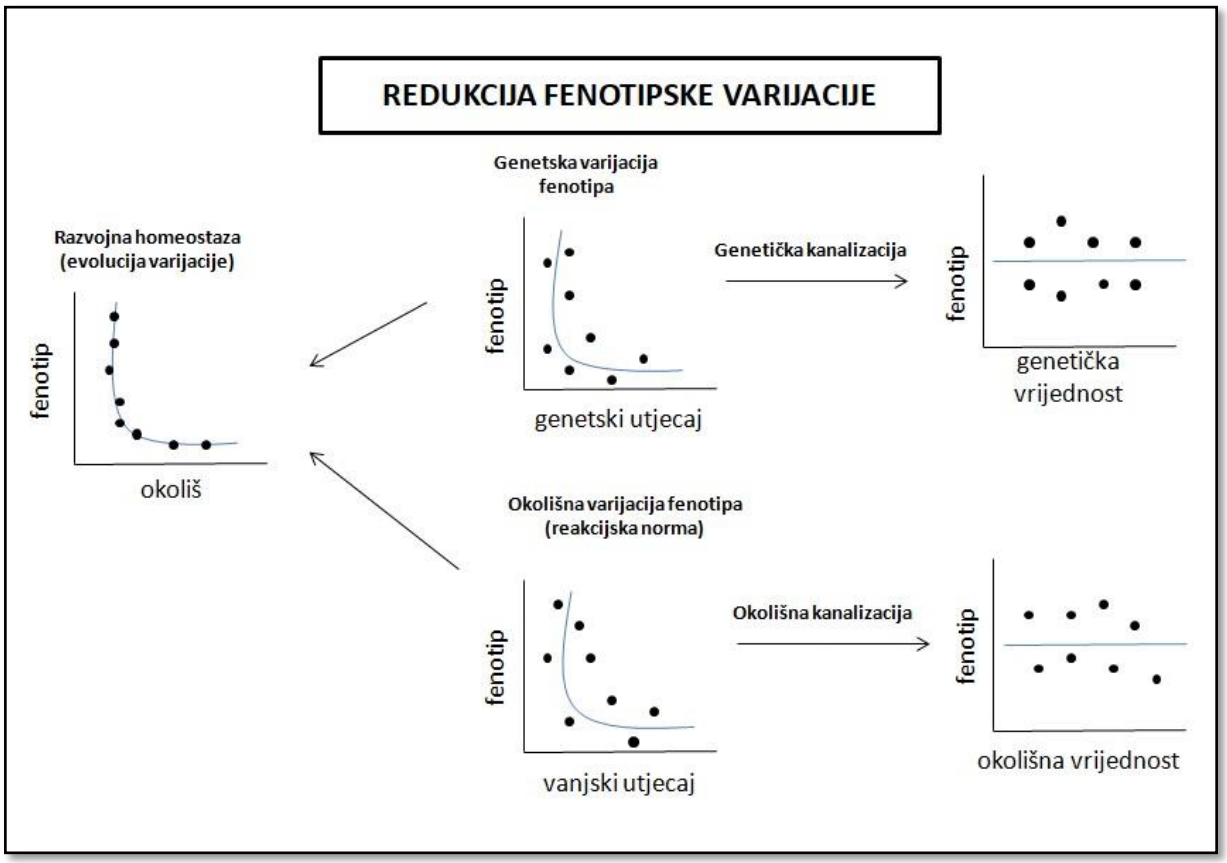
1.3.5. Razvojna nestabilnost

1.3.5.1. Vrste fenotipskih varijacija

U biologiji riječ asimetrija označava sastav tijela organizma iz potpuno jednakih dijelova (npr. lijeva i desna strana ljudskog tijela ili krila leptira). Međutim, bilateralna simetrija živih organizama često nije potpuna pa se lijeva i desna strana iste jedinke razlikuju. Razvoj lijeve i desne strane kod malih organizama ili u ranim embrionalnim stadijima događa se kao razvoj jednog razvojnog polja. Kod većih organizama razvoj strana događa se neovisno jedan o drugom kada ometajući faktori jedne strane neće utjecati na normalan razvoj druge. Obje strane su pod utjecajem jednakih genetički razvojnih mehanizama, ali nisu nužno pod jednakim okolišnim utjecajem. Zbog toga će konačan izgled fenotipa ovisiti i o genetičkim i o okolišnim promjenama (75).

Kako bi se prepoznala nastala fenotipska varijacija, uveden je pojam ciljnog fenotipa. Pod tim pojmom podrazumijeva se izgled organizma koji je određen poznatim i predvidljivim genetičkim promjenama u uvjetima okoline bez ometajućih čimbenika i s potpunim odsustvom varijacija.

Postoje dvije vrste fenotipske varijacije. Prva je sistemska varijacija fenotipa s okolišnim i genetičkim varijacijama (**Slika 6**.). Proces kojim se struktura organizma razvija prema ciljnom fenotipu, pod različitim genetičkim i okolišnim uvjetima naziva se kanalizacija. Genetička varijacija fenotipa ovisi o genetičkoj kanalizaciji, tj. o procesu smanjivanja osjetljivosti struktura ili organizma na razini smanjivanja senzitivnosti alela (76). Ovo smanjenje posljedica je modifikacije veličine alela, ali se pretpostavlja da broj i vrsta segregacijskih lokusa ostaju konstantni (77, 78, 79).



Slika 6. Sistemska varijacija fenotipa s genetičkim i okolišnim varijacijama (autorsko djelo).

Genetička varijacija fenotipa ovisi i o okolišnoj kanalizaciji, tj. o procesu koji dovodi do smanjenja osjetljivosti strukture ili organizma na djelovanje okoliša (npr. temperatura ili hranjive tvari). Pojam suprotan kanalizaciji je fenotipska plastičnost, a koristi se za opisivanje fenotipske varijacije koju proizvodi genotip kao odgovor na varijaciju okoliša. Vrsta fenotipske plastičnosti je reakcijska norma kojom se opisuje više kontinuiranih različitih fenotipova proizvedeni genotipom, kao odgovor na različite uvjete okoliša (80, 76).

Druga vrsta fenotipske varijacije je varijacija oko ciljnog fenotipa koja se može vizualizirati kao raspršivanje oko ciljnog fenotipa i predstavlja neuspjeh u postizanju istog. Ova vrsta fenotipske varijacije zove se razvojna nestabilnost (81).

1.3.5.2. Čimbenici nastanka razvojne nestabilnosti

Razvojna nestabilnost može nastati zbog triju razloga. Prvi je nepoznat, uslijed nepotpunog poznavanja složenog međudjelovanja različitih čimbenika koji djeluju u formiranju sustava. Drugi je zbog stohastičnih razvojnih događaja te se općenito prihvaća kao glavni uzrok razvojne nestabilnosti i razvojno inducirane fluktuacijske asimetrije. Treći, donedavno neistraženi, izvor fluktuacije asimetrije je okolišno inducirana asimetrija (82).

1. Nepotpuno poznavanje razvojnog sustava

Ako se pojedinci ljudske populacije razlikuju u odnosu na gene čiji učinak na svojstvo ne znamo i stoga ga ne možemo kontrolirati, pojavit će se slučajna fenotipska varijacija oko nekog pretpostavljenog idealnog fenotipa. Ta varijabla nema utjecaj na magnitudu fluktuirajuće asimetrije. Sustav se može razviti da bude manje (ili više) osjetljiv na nepoznate i nekontrolirane čimbenike u genetičkom ili fizičkom okruženju, ali se njihova varijacija ne izražava kao fenotipska varijacija. Varijacija se događa smanjenjem broja alela koji kodiraju fenotip, bilo fiksiranjem ili snižavanjem njihove frekvencije, dok se prosječna magnituda alelnih utjecaja ne mijenja (77).

2. Razvojno inducirana asimetrija

Varijacija koja je posljedica stohastičnog razvoja je jedini stvarni uzrok fluktuacijske asimetrije zbog toga što svaka polovica bilateralno simetričnog organizma predstavlja razvojnu jedinku u kojem stohastičke komponente djeluju samostalno. Da bi se shvatilo kako se može pojaviti i mijenjati fluktuacija asimetrija, potrebno je razumjeti uzroke neodređenosti u razvoju, gdje dolazi do razvojnih stohastičkih varijacija i kako sustav može biti više ili manje osjetljiv na nju (83).

Ne postoji jedan opći uzrok stohastičnosti, već postoje različiti specifični, često jedinstveni procesi koji utječu na sustav na slučajan način. Izbor uzročnog morfogenetičkog signala između različitih alternativnih razvojnih puteva mogao bi biti sklon pogreškama. Isto tako, ako je gradijent morfogena ili neke druge razvojne determinante relativno mali, teško je odrediti prag koji će dovesti do promjena. Jednostavno vizualizirani primjer ove pojave

događa se u uzorcima boja leptira, pri čemu ljestvice koje nose pigment moraju „odlučiti“ napraviti jedan pigment ili drugi. Stanice na rubu između područja kontrastnih boja često pogrešno čitaju gradijent, a ljestvice „pogrešne“ boje su uobičajene. U područjima gdje je normalan postupni prijelaz između boja, ovaj se prijelaz očituje kao dvostruka promjena udjela vage dviju boja. Točni detalji tih stupnjeva boja različiti su na lijevoj i desnoj strani jer su različiti izbori učinjeni kada gradijent nije jasno odredio boju. U biološkoj genetički stabilnoj strukturi gdje bi izolirane stanice koje čine potpuno „pogrešnu“ radnju trebale ne preživjeti, u ovom slučaju različito čitanje plitkog gradijenta boja rezultirat će pojednostavljenim pozicioniranjem stanica krila leptira u dvije populacije ovisno o različitom stanju kompenzacije, odnosno ovisno o dvama različitim odabirima čitanja boje. To bi se pak u biološkom tkivu moglo manifestirati kao male stohastičke razlike u veličinama ili oblicima tkiva, organa i u konačnici nastanka asimetrije među njima. Jedino objašnjenje nastanka ovakvih fenotipskih varijacija je razvojna nestabilnost (84, 85).

Prema istraživanju koje su proveli Thornill i Moller (1997.), asimetrija može nastati kao posljedica promjena na trima razinama: genskoj, kromosomskoj i proteinskoj. Fluktuacijska asimetrija s genskim poremećajima može biti povezana putem različitih mehanizama: 1) kromosomske abnormalnosti, 2) štetni geni koji nastaju mehanizmom mutacija mogu poremetiti razvoj genetičkom smetnjom unutar ukupne zalihe gena, a ukoliko su recesivni, uklanjanje iz ukupne zalihe gena populacije putem prirodne selekcije je otežano, 3) geni koji imaju pozitivan ili neutralan utjecaj mogu na razvoj organizma imati negativan ukoliko se okoliš promjeni; 4) evolucija direktnom selekcijom može povećati frekvenciju novih ili rijetkih alela u ukupnoj zalihi gena izazivajući poremećaje koji će povećati fluktuacijsku asimetriju (86).

Danas se razvojna regulacija ponajbolje objašnjava terminom genetičkih krugova. Oni predstavljaju mrežu (ili poveznicu) genetičke aktivacije i suzbijanja koje rezultiraju određenim razvojnim efektom. Ovaj se mehanizam sastoji od kaskada regulatornih gena. Neki od ovih gena kodiraju regulatorne proteine koji djeluju lokalno i reguliraju privremeni obrazac genske ekspresije. Drugi kodiraju transkripcijske regulatore koji su puno šire rasprostranjeni i reguliraju prostorne obrasce genske regulacije. Ti krugovi mogu sadržavati pozitivne i negativne petlje i različite varijacije nelinearnih procesa. Ako je nivo transkripcijskih čimbenika koji reguliraju prepisivanje gena veoma mali, i mala varijacija u njihovoj koncentraciji, koja bi inače bila zanemariva da je ukupni koncentracijski nivo veći,

može dovesti do promjene vjerojatnosti u djelovanju razvojnog prekidača (85). Ovo se može vidjeti na svakom razvojnom mehanizmu u kojem odgovor „sve ili ništa“ ovisi o malom broju događaja (ili bilo kojeg postupka koji je reguliran interakcijom između malog broja molekula). Slučajna promjena u rijetkim genetičkim događanjima dovodi do slučajne promjene izlazne radnje i konačnog nusprodukta. Konačno, slučajna varijacija konačnog izgleda fenotipa može proizaći i iz kaotičnih procesa (87). Kaotične sustave karakterizira velika osjetljivost na početne razvojne uvjete pa je moguće da bi i male varijacije početnih uvjeta mogle bitno promijeniti ishode kaotičnog razvojnog mehanizma u različitim dijelovima organizma što se može očitovati kao fluktuirajuća asimetrija. Slučajni obrasci, kao što su pruge tigra, zebre ili žirafe te mrlje leoparda, pa i ljudski otisci prstiju proizvod su velike osjetljivosti na slučajnu varijaciju u početnim uvjetima razvoja (88).

Dodatno u interakciji s regulatornim genima različiti kemijski i fizički procesi imaju ontogenetsku ulogu. Neki od njih su: difuzija, morfogenetički pokreti, migracija stanica, kemija ekstracelularnog matriksa, programirana smrt stanice i cijeli niz enzimatskih reakcija. Mnogi, ako ne i svi, procesi u razvoju pod utjecajem su temperature, pH, prisutnosti nutritijenata, radijacije, gravitacije i fotoperioda. Varijacija bilo kojeg od navedenog može rezultirati konačnim ontogenentskim varijacijama fenotipa (89).

3. Okolišno inducirana fluktuacijska asimetrija

Osim genetičkih, značajnu ulogu u ontogenetskom razvoju prema najnovijim istraživanjima imaju i okolišni čimbenici (90, 91). Organizam koristi mnogostruke mehanizme modifikacije za unaprjeđenje i bolju prilagodbu na vanjske uvjete života. Prema Waddingtonovoj „teoriji kanaliziranja“ prirodna selekcija dozvoljava translaciju genotipa u fenotip kao jedan stabilan uniformni proces razvoja organizma. Takvi stabilni razvojni modeli dozvoljavaju organizmu da ispolji određen stupanj okolišne varijabilnosti. Ipak, vanjski utjecaji u određenoj mjeri mogu poremetiti proces razvoja organizma (92). Pojedinac koji ima savršeno simetrične morfološke osobine posjeduje kapacitet gena koji je otporan na razvojne poremećaje ili pak razvojni poremećaji nisu dovoljnog intenziteta da naruše normalnu morfogenezu. Najčešće nepovoljni okolišni utjecaji na organizam tijekom njegovog razvoja mogu biti mehanički i kemijski, zatim prehrambeni poremećaji, poremećaj hormonskog sustava majke, manjak kisika, infekcije i socioekonomski faktori (93, 94.). Usprkos jasnim pokazateljima utjecaja

nepovoljnih okolišnih čimbenika na nastanak asimetrije, ne treba zaboraviti da je genetički sustav okvir koji tim čimbenicima dozvoljava utjecaj na formiranje konačnog fenotipa.

Starija su uvjerenja bila da okolišni čimbenici mogu uzrokovati promjene unutar jedne strane strukture, ali ne sudjeluju u nastanku asimetrije te da nije moguće razlikovati okolišno induciranu fluktuacijsku asimetriju od fluktuacijske asimetrije nastale zbog ometajućih razvojnih faktora, osim ako nema izravnih dokaza da dvije polovice organizma ne doživljavaju različite mikropromjene (95, 96). Također se vjerovalo da se zbog procesa prilagodbe i mehanizama održavanja homeostaze, a pod utjecajem najlakše promijenjivih okolišnih čimbenika može čak „umjetno“ pokušati ublažiti asimetriju nastalu kao rezultat razvojne nestabilnosti (97).

1.3.5.3. Fluktuacijska asimetrija kao pokazatelj razvojne nestabilnosti

Uvriježena su mišljenja da povećana asimetrija ukazuje na neuspjeh organizma u održavanju razvojne homeostaze i prevladanje okolišnih poremećaja nad genetičkim kontrolnim mehanizmima (98). Razvojna stabilnost označava otpornost organizma na različite poremećaje koji mogu snaći organizam tijekom rasta i razvoja, a možemo ju izraziti blagim slučajnim odstupanjima od bilateralne simetrije (99). Budući da fluktuacijska asimetrija nastaje uslijed nesposobnosti organizma da omogući lijevoj i desnoj strani da se jednako razviju, često se u istraživanjima koristi kao mjera razvojne nestabilnosti koja nastaje tijekom razvoja organizma (100, 95). Tako se fluktuacijska asimetrija direktno povezuje s modifikacijom imunološkog odgovora na cjepivo i općenito s uspješnošću odupiranja organizma infekcijama (101). Marado i Silva (2016.) utvrdili su veću učestalost fluktuacijske asimetije kod umrlih od posljedica zaraznih bolesti, uglavnom tuberkuloze, u odnosu na umrle od ostalih uzroka (102).

Razvojna stabilnost je sposobnost organizma da trasformira informaciju pohranjenu u genotipu u fenotipski identični oblik pod postojećim okolišnim uvjetima u kojima se organizam razvija, sve devijacije navedenog procesa nastaju kao posljedica genetičkih i okolišnih pritisaka kojima je organizam izložen tijekom rasta i razvoja. Navedeni pritisci obično se mogu prepoznati kao razvojni poremećaji ili fenodevijacije, odnosno velike razvojne greške ili kao različite minor anomalije (86).

Živi organizam tijekom razvoja, ali i kasnije, koristi mnogostruke mehanizme modifikacije kako bi se prilagodio na vanjske uvjete života. U razvoju lica mnogo je trenutaka kada je osjetljivost na okolišne čimbenika izrazito visoka (103). Fluktuacijska asimetrija uglavnom se javlja kod poligenetičkih svojstava, odnosno kod skupa gena koji više ili manje ravnomjerno pridonose konačnom definiranju pojedinog obilježja, baš kao što je i primjer lica. Kako njihov učinak ne proizvodi dovoljan diskontinuitet za individualno proučavanje segregacije (104), upravo proučavanje fluktuacijska asimetrija kod različitih svojstava, a kod unaprijed definirane populacijske skupine, može poslužiti kao pokazatelj genetičke stabilnosti organizma.

Na povezanost genetičkih svojstava s obilježjima lica i fluktuacijske asimetrije ukazano je u mnogim istraživanjima. Graber (4) sumira rezultate ranijih istraživanja i zaključuje da nasljeđe igra ulogu u određivanju sljedećih obilježja: kongenitalnih anomalija, facijalne asimetrije, makrognatije i mikrognatije, makrodoncije i mikrodoncije, hiperdoncije i hipodoncije, varijacije u obliku zuba, rascjepa usne i nepca, središnje dijasteme (diastema mediana) i duboke insercije frenuluma, dubokog zagriza, zbijenosti, mandibularne retrognatije i prognatije te utvrđuje kako su navedena obilježja uglavnom poligenska (Graber, 1972). Weinberg je koristeći 3D fotogrametriju pokazao koji aspekti lica imaju najveći utjecaj nasljeđa te je među njima naveo i asimetriju (105).

Mjerenje fluktuacijske asimetrije je laboratorijski postupak *in vivo* za mjerenje razvojne stabilnosti organizma i najsenzibilniji indikator sposobnosti organizma da se odupre okolišnim poremećajima tijekom ontogeneze. Mogućnost odupiranja okolišnim poremećajima tijekom rasta i razvoja veća je kod organizama koji imaju veći fond gena ili gensku zalihu što se očituje u tzv. genetičkoj heterozigotnosti (106). Budući da je do sada ukazano na značajnu ulogu nasljeđa u razvoju lica, istraživanje razvojne stabilnosti fenotipa lica ukazalo bi na odnos i međudjelovanje genetičkih i okolišnih čimbenika tijekom rasta i razvoja kraniofacijalnog sustava.

1.3.5.4. Direkcijska asimetrija kao pokazatelj razvojne nestabilnosti

Direkcijska asimetrija i antisimetrija često se u studijama javljaju s fluktuacijskom asimetrijom. Sve tri vrste asimetrije dinamički su međusobno povezane (74). Također, prijelazi iz jednog oblika asimetrije u drugi su uobičajeni, a o tome je izvijestio (107) koji je

promatrao prijelaz iz direkcijske asimetrije u fluktuirajuću asimetriju, kada je prešao dvije inbred linije Dosophila. Oba oblika asimetrije predstavljaju fenotipsku varijaciju vrijednu proučavanja.

Ako se ukupna asimetrija može podijeliti na direkcijsku i fluktuirajuću komponentu, onda se može početi shvaćati kako bilateralna simetrija ne postoji. Na primjer, mijenja li se fluktuirajuća asimetrija ako bilateralna simetrija ne postoji? Štoviše, je li direkcijska asimetrija genetski viša varijabla (tj. više razvojno stabilna) od bilateralno simetričnih znakova?

Odgovori na ova pitanja zahtijevaju način procjene razvojne nestabilnosti u smjeru asimetričnih osobina. Za to je potrebno procjeniti srednje razvojnu putanju smjera asimetrične osobine i procjeniti slučajnu varijaciju oko te putanje. Mnoga istraživanja tu rezidualnu varijaciju interpretiraju kao razvojnu nestabilnost, možda kao odgovor na neki stres. Ali stres može promijeniti i oblik srednje putanje.

Postoje brojni primjeri promjena razvoja pod utjecajem okolišnog stresa. Na primjer, (108) pokazali su kako biljka imena Luciliu cupnnu prilikom prilagodbe na insekticid Diazinon prolazi kroz prijelaz od fluktuirajuće asimetrije do antisimetrije i natrag. Graham i suradnici (109) pokazali su da je Drosophila melanogaster izložena povećanim koncentracijama benzena prijelazi iz fluktuirajuće asimetrije u smjeru asimetrije. Hallgrimsson i suradnici (110) pokazali su da velike plave čaplje (Ardeu herodim) izložene toksinima pokazuju veću intercerebralnu asimetriju smjera. Rowe, Repasky i Palmer (111) pokazali su da je nekoliko seksualno odabranih osobina u literaturi prijavljeno kao fluktuirajuća asimetrija zapravo pokazuje antisimetriju ovisnu o veličini.

Budući da se razvojna putanja može mijenjati pod stresom, najispravnije ju je promatrati kao najbolju prilagodbu, a varijacije fenotipa i oblika shvaćati kao raspodjelu oko te putanje.

Svi ostaci koji mogu postojati su aditivna genetska varijacija ili okolišna varijacija koja utječe na intenzitet bilo direkcijske asimetrije ili antisimetrije. U tom slučaju ne proporučuje se koristiti direkcijsku asimetriju kao procjenu razvojne nestabilnosti.

Dok direkcijska asimetrija i razlika u pozicijskim signalima između dvije strane tijela predstavljaju izazov za centralni argument principa nastanka fluktuacijske asimetrije jer se odgovarajuće strukture lijeve i desne strane ne razvijaju pod identičnim uvjetima, ova tvrdnja vjerovatno neće uzrokovati ozbiljne praktične poteškoće. Ovaj direktni efekt direkcijske

asimetrije može se jednostavno uklopiti: fluktuacijska asimetrija tada se promatra kao devijacija asimetrične forme individualca od prosječne asimetrije (odnosno od direkcijskog očekivanog utjecaja na genotip i na uvjete rasta).

Obje strane iste jedinke su pod jednakim utjecajem razvojne nestabilnosti i to je razlog zašto je direkcijska asimetrija najčešće mala: razvojni procesi lijeve i desne strane približno su jednaki i sistem će propoznati moguće veće promjene jedne strane na jednaki način.

Ako je morfološka simetrija primjetna, moguće je da je asimetrija tijekom razvoja toliko velika da dvije strane tijela ne mogu upravljati intrizičnim kontrolama i zato je nastala simetrija kao mjera razvojne nestabilnosti.

U većini studija flutuacijske asimetrije, direkcijska je toliko mala i razvojne razlike su toliko malene da fluktuacijska preostaje kao jedina mjerljiva razlika između lijeve i desne strane kao mjera razvojne nestabilnosti.

Neki autori sugeriraju i moguće mjerenje direkcijske asimetrije kao mjere razvojne nestabilnosti (72, 74, 112) Budući da je direkcijska srednja asimetrija uzorka, ona ne predstavlja morfološke promjene nastale kao posljedica uznemirujućih faktora za vrijeme razvojne nestabilnosti. Ako se promjeni neki okolišni faktor, rezultat je promjena direkcijske asimetrije jer je taj stres djelovao i na lijevu i na desnu stranu tijela, kao razvojni odgovor na okolišne faktore, ovisno o pozicijskim signalima koji reguliraju razlike između lijeve i desne strane.

Zbog toga je varijacija direkcijske asimetrije s razvojnim faktorima poseban primjer reakcijske norme, nešto što utječe na obje strane tijela, ali se ne može povezati s razvojnom nestabilnošću.

1.4. Izolirane populacije i genetička raznolikost

1.4.1. Izolati u istraživanjima kompleksnih svojstava

Reproduktivno i geografski izolirane populacije pogodne su za proučavanje rasta i razvoja, poremećaja i bolesti poligenskog nasljeđivanja. Razlog za to je ograničeni genski bazen (113), odnosno dijeljenje limitiranog fonda gena unutar izolirane populacije. Također, izolirane populacije imaju ograničenu raznolikost okolišnih čimbenika što ima posebno značenje u kontekstu međuodnosa genetičkih i okolišnih utjecaja, odnosno moguće je lakše

prepoznati, i za potrebe istraživanja izolirati, pojedini remetilački faktor razvoja jer populacija dijeli zajedničke okolišne čimbenike (114).

Konačni cilj genetičke epidemiologije je identificirati i karakterizirati populacijske faktore kao uzročnike određene bolesti, odnosno fenotipskog obilježja (115). Danas su prihvaćena tri pristupa genetičkih istraživanja: analiza relativne zahvaćenosti dvaju ili triju genetičkih parova (najčešće zahvaćenost parova, tzv. nelinearna povezanost), analiza povezanosti mnogobrojnih genetičkih faktora između brojnih obitelji i u posljednje vrijeme analiza obitelji genetički izoliranih populacija (116). Prvi pristup, analiza parova, ima limitirajuću vrijednost za detekciju malih genetičkih efekata koji se povezuju s najčešćim kompleksnim bolestima. Studije velikih obitelji pokazale su se uspješne za identifikaciju malih genetičkih utjecaja u slučaju poznatih bolesti kada je glavni hereditarni učinak poznat (117). Najnoviji pristup proučavanja izoliranih populacija pokazao se iznenađujuće uspješan za mapiranje haplotipova. Ovim genetičkim pristupom mapiraju se točno ciljana genotipska i fenotipska obilježja odabranih pojedinaca i njihovih poznatih predaka. To je moguće jer se traženi haplotipovi pretka te populacije mogu identificirati metodom mapiranja homozigota za recesivna svojstva (118, 119, 120).

Istraživanja Mendelovih bolesti koje su determinirane poremećajem jednog gena veoma su napredovala. Nasuprot tome, istraživanja genetičke podloge kompleksnih bolesti i kompleksnih svojstava, kao što je primjerice maksilofacijalna varijacija, i dalje su izazov za suvremenu medicinsku genetiku. Zato su izolirane populacijske skupine izvrstan model za istraživanja utjecaja i nastanka kompleksnih bolesti, odnosno kompleksnih morfoloških, fizioloških i psiholoških obilježja (121).

Činjenica koja upućuje na važnost genetičkih čimbenika u etiologiji neke bolesti ili fenotipske karakteristike, kao što je primjerice asimetrija lica, upravo je njihova povećana učestalost u genetički zatvorenoj populaciji te u populaciji s visokom proporcijom krvno srodnih brakova, tj. populaciji koja je karakterizirana povećanim tzv. koeficijentom srođivanja (*inbreedinga*) (122). Srođivanje samo po sebi nije uzrok nastanka bolesti niti povećane učestalosti kompleksnih obilježja kao što je npr. asimetrija lica, već ono povećava vjerojatnost nasljeđivanja istih alela od roditelja koji su u krvnom srodstvu nego među onima koji to nisu, odnosno vjerojatnost nasljeđivanja kakva bi bila u mješovitoj, ili kako se često naziva, panmiktičnoj popuaciji (123). Dakle, povećava se vjerojatnost susretanja dvaju rjeđih mutiranih recesivnih alela koji u homozigotnom obliku mogu doći do fenotipskog izražaja. To

ovu skupinu čini „genetički manje stabilnom“, a kao mjera te nestabilnosti vrlo često se koristi stupanj fluktuacijske asimetrije različitih obilježja (49).

Blisko krvno srodstvo među bračnim partnerima je u pojedinim područjima svijeta vrlo izraženo. Samo jedan primjer među mnogim su palestinski Arapi gdje stupanj konsangviniteta raste na gotovo 44,3 % brakova (124). Također, česti su primjeri i među različitim izoliranim populacijama na svim kontinentima (125) pa tako i u Europi (126, 127.) i u Hrvatskoj (128). Važnost poznavanja utjecaja recesivnih gena na organizam u cjelini, ali i na pojedine organe i organske sustave, vidi se u podacima da je stupanj konsangviniteta među roditeljima bolesnika s rijetkim autosomalnim recesivnim poremećajima značajno veći nego u općoj populaciji (129).

1.4.2. Dalmatinski izolati i povijesne okolnosti njihove izoliranosti

Zemljopisna, reproduktivna i genetička izoliranost čini stanovništvo srednjodalmatinskog otočja pogodnim modelom za istraživanja o ulozi genetičkih i okolišnih čimbenika u etiologiji, fenotipskoj varijaciji i progesiji određenih kompleksnih bolesti ili kompleksnih svojstava (130).

Jadransko otočje čini sveukupno više od 1 000 otoka i većina njih su veoma malene zemljopisne površine na usko ograničenom području koje ima relativno ujednačenu i neveliku raznolikost okolišnih čimbenika koje sustavno djeluju na populacije koje ih naseljavaju (129. 131). Od ukupnog broja otoka tek 47 ih je naseljeno, ali mnogi od njih samo s nekoliko obitelji. U sjevernu grupu od većih otoka spadaju: Krk, Cres, Lošinj, Rab, Pag, Ugljan, Pašman i Dugi Otok, dok u južnu spadaju: Brač, Šolta, Hvar, Korčula, Vis, Lastovo i Mljet. Sveukupno na tim otocima živi 125 281 stanovnika i to većinom starog stanovništva, starijeg od 60 godina.

Pučanstvo otoka srednje Dalmacije primjer je posljednjih genetički izoliranih populacijskih skupina u današnjoj Europi. Tu još uvijek nalazimo niz malih, prvenstveno reproduktivnih, izoliranih podpopulacijskih skupina koje su posebice pogodne za razmatranje (mikro) evolucije srednje dalmatinskih otoka s različitih gledišta (130). Posebnost podpopulacija otoka ogleda se u, prije svega, dvije dominantne pojave koje otoke čine izvrsnim modelima za proučavanje multidisciplinarnih studija evolucijskih procesa: pojave dihotomnosti i pojave izoliranosti koje su uvjetovane specifičnim povijesnim i zemljopisnim okolnostima. Uz

postojeću geografsku, također je prevladavanje reproduktivnih veza unutar pojedinih naselja uzrokovalo i unutarnju reproduktivnu izoliranost (132). Populacije otoka imaju i vrlo slične okolišne čimbenike (prehrana, klimatske promjene, medicinska zaštita, stomatološka skrb, obrazovanje) pa se okolišna varijanca smanjuje u ukupnoj fenotipskoj varijanci (128).

Na specifičnu populacijsku strukturu otoka srednje i dijela južne Dalmacije utjecala su složena povijesna previranja još od doba prvih naseljavanja pa sve do danas.

Za današnju populacijsku strukturu srednjodalmatinskog otočkog stanovništva posebno je važno razdoblje od 15. do 18. st kada je došlo do intenzivnog prodora Turaka. Posljedice toga jesu snažne migracije stanovništva iz kopnene unutrašnjosti prema jadranskom primorju i otocima koji su bili sigurnije utočište stanovništvu Bosne, Zagore i Makarskog primorja (131). Došljaci tada donose nove gene i kulturna obilježja. Tada dolazi i do miješanja štokavskog narječja došljaka s čakavskim narječjem starosjedioca. Drugi veliki val naseljavanja razdoblje je Kandijskih ratova između 1645. i 1669. godine. U to vrijeme Makarani se bore na strani Mletaka dobivši time dozvolu da im se obitelji smiju skloniti na otoke. Svim doseljenicima Mletačka Republika dala je posebne privilegije (tzv. „privilegije Paštrovića“), oslobodila ih je javnih radova i plaćanja poreza i carina te rada na galijama. Navedene privilegije izgubili bi jedino ako bi se oženili sa starosjediocima što je utjecalo na povećani animozitet između starosjedioca i doseljenika te je dovelo do reproduktivne zatvorenosti među njima. Izjednačavanje prava starosjedioca i doseljenika postiže se tek dva i pol stoljeća kasnije dolaskom Napoleona Bonapartea i francuske vlasti i ukinućem svih privilegija (133).

1.4.3. Antropološke studije genetičke strukture na dalmatinskim izolatima

Do sada je napisano preko 200 znanstvenih publikacija nastalih istraživanjem ovih populacija. Njihove genetičke izoliranosti najbolje se ogledaju u podacima koje opisuju stupnjeve endogamije, odnosno u procjenama stupnja srođivanja unutar pojedinih populacija (**Tablica 3**).

Tablica 3. Usporedba koeficijenta srođivanja dobivenih iz podataka izonimije u usporedbi s pojedinim svjetskim popuacijama (preuzeto iz Rudan I i suradnici, 2006) (128).

COMPARISON OF INBREEDING COEFFICIENT ESTIMATED FROM THE ISONYMY DATA IN THIS STUDY WITH THE REPORTED DATA IN SELECTED WORLD POPULATIONS

Author	Population	Inbreeding coefficient
Lasker, 1977 (18)	Peru	0.0040
Kayshap and Tiwari, 1980 (19)	Kashmir	0.0400
Wilson, 1981 (20)	Bhatia	0.0427
Hurd, 1983 (21)	Nebraska Amish	0.1129
Lasker, 1985 (22)	Reading, England	0.0003
Sujoldžić, 1989 (23)	Island of Silba, Croatia	0.0110
Sujoldžić, 1989 (23)	Island of Olib, Croatia	0.0162
Biondi et al., 1990 (24)	Greek villages in Italy (Calabria)	0.0144
Biondi et al., 1993 (25)	Albanian villages in Italy	0.0063
Sujoldžić, 1993 (26)	Island of Korčula, Croatia	0.0244
De Braekeleer, 1996 (27)	SLSJ region, Quebec, Canada	0.0069
Roguljić et al., 1997 (28)	Island of Hvar, Croatia	0.0233
Rudan et al., 1999 (29)	Island of Pag, Croatia	0.0331

Prema podacima opisanim u radu (128) na sveukupno 10 000 stanovnika 7 otoka, sveukupno jednoj trećini ukupne otočke populacije napravljena su brojna antropometrijska mjerenja. Istraživanja i analize pokazale su kako postoji tzv. izolacija s udaljenošću, tj. uočene su razlike otočkih podpopulacijskih skupina u povijesnim i demografskim kretanjima, trendovima migracije stanovništva te pri različim kompleksnim svojstvima kao npr. u prostoru kvalitativnih i kvantitativnih svojstava dermatoglifa digitopalmarnog kompleksa, u morfološkim svojstvima stanovništva, u fiziološkim svojstvima stanovništva, u morfometrijskim analizama metakarpalnih kostiju, analizama eritocitnih antigena i serogenetičkih polimorfizama, ali i u društvenim aspektima kao što su svojstva bazičnog i kulturnog rječnika i izonimiji te u genetičkim istraživanjima VNTR, mt DNA i kromosoma Y (134, 135, 136).

Kao što je iz dosadašnjih istraživanja vidljivo, navedene osobitosti hrvatskih otoka pokazuju jasnu reproduktivnu izoliranost uz relativnu jednolikost okolišnih čimbenika. Naravno, kada se govori o različitim otocima, ne može se govoriti o potpunoj ujednačenosti niti reproduktivne izoliranosti niti okolišnih čimbenika. Demografska povijest svake otočne zajednice razlikuje se ovisno o vremenu osnivanja, podrijetlu i broju osnivača, događajima, duljini izolacije i fluktuirajućim promjenama u veličini populacije. Sve te karakteristike utječu na opseg genetičke diferencijacije i obrasce povezivanja unutar svake populacije, kao i na slučajni genetički pomak i razinu endogamije i inbreedinga (128).

Tako, primjerice, studija rađena na više malih, izoliranih populacija („metapopulacija“) na otocima Dalmacije u razdoblju do 2002. do 2003. godine sastojala se od analiza nasumično odabranih 100 pojedinaca iz 10 malih otočnih naselja (oko 2 000 stanovnika) - Banjol, Barbat, Lopar, Rab, S Draga, Vis, Komiža, Lastovo, Mljet, Susak (136). Otočne zajednice predstavljaju jedinstveni široki raspon različitih i dobro dokumentiranih demografskih povijesnih podataka. Njihova genetička svojstva analizirana su upotrebom 26 kratko ponavljajućih markera (STR), ne manjih od 5cM. Pronađena je veoma visoka razina diferencijacije između većine otočnih zajednica, čak i unutar pojedinog otoka. Definirano je i šest klastera s vrlo različitom genetičkom kartom, od kojih su 4 odgovarale pojedinačnim selima.

Genetski lokusi su u neravnoteži (*linkage disequilibrium*) kada je učestalost povezivanja njihovih različitih alela veća ili manja od one koja bi se očekivala da su lokusi neovisni i nasumično povezani (138). Ta genetska neuravnoteženost utječe na mnoge čimbenike: selekcija, brzinu genetske rekombinacije, stopa mutacija, genetski pomak, sustav parenja, struktura populacije i genetsku povezanost. Obrazac neravnoteže povezanosti u genomu moćan je signal populacijskih genetičkih procesa koji ga strukturiraju.

Razina tzv. *linkage disequilibrium* procjenjivana je s osam povezanih markera na Xq 13-21 i u većini ispitivanih populacija bila je vrlo visoka (137).

Snažna izolacija i endogamija glavni su razlozi visoke genetičke specifičnosti ovih populacija i pojave specifičnih autohtonih bolesti i različitih medicinskih poremećaja (128).

Treba napomenuti kako srođivanje samo po sebi nije uzrok genetičkim poremećajima. Jedini pravi genetički uzrok povezan sa srođivanjem jest spoznaja da postoji veća vjerojatnost nasljeđivanja istih alela kod osoba koji potječu iz brakova među srodnicima nego onih koji to nisu. Stoga srođivanje povećava vjerojatnost susretanja dvaju rijetkih mutiranih recesivnih gena u homozigotnom obliku (128). Neželjeni fenotip nastao kombinacijom recesivnih alela koji mogu, ali i ne moraju biti poremećeni, u homozigotnom obliku fenotipski dolaze do izražaja. Stoga, osobe koje potječu iz brakova među srodnicima mogu fenotipski biti normalne i bez ikakvih posljedica ako su u homozigotnom obliku naslijedili nemutirane recesivne gene. Međutim, kod kompleksnih bolesti i kompleksnih obilježja situacija za nastanak je nešto složenija. U nastanku kompleksnih bolesti (povišen krvni tlak, sklonost malignim oboljenjima), kao i kod različitog ispoljavanja kompleksnih obilježja, (npr. asimetrija lica) više gena koji imaju aditivni učinak imaju dodatno povećanu vjerojatnost za

manifestaciju fenotipskog učinka. Zbog toga ne čudi da na hrvatskim otocima nalazimo specifične genetičke poremećaje kao što su mljetska bolest ili Mal de Meleda sindrom, tj. recesivna parmoplantarna keratodermatoza koja se prvi put javila na Mljetu 1397. godine, a od ukupnog broja oboljelih evidentirano je samo nekoliko slučajeva izvan područja Mljeta i to u Italiji, Tunisu, Saudijskoj Arabiji i u Ujedinjenim Arapskim Emiratima (139). Svi oni mogli su trgovačkim putevima biti u kontaktu sa stanovnicima otoka Mljeta. Potom, nasljedni patuljasti rast ili priobalni primorski kretenizam koji je oblik nanizma zabilježen samo u Bašćanskoj Dragi i Juran Dvorima. Sveukupno se zna za 23 oboljele osobe i sve su bile stanovnici dvaju navedenih sela. Također, dobro je poznat izraziti konsangvinitet otoka Suska gdje je na 1 400 ispitanika koji imaju samo 7 različitih prezimena pronađen značajno veći postotak krvne grupe A, Rh minus faktora te visok stupanj različitih poremećaja kao npr. visok krvni tlak te česte psihičke bolesti (shizofrenija, senilna demencija, psihoza) (128).

Od kompleksnih bolesti posebno su značajna istraživanja malignih bolesti koje je proveo Rudan (114) te je utvrdio povećanu učestalost karcinoma na području pet otoka: Brač, Hvar, Korčula, Vis i Lastovo.

Iz svega navedenog može se isčitati kako zemljopisna, reproduktivna i genetička izoliranost čini pučanstvo srednjodalmatinskih otoka iznimno prikladnim modelom za istraživanja o ulozi genetičkih čimbenika u etiologiji i progresiji različitih kompleksnih poremećaja. Stoga su istraživanja jadranskog otočja vrlo pogodna za atropološka istraživanja od kojih su neka usmjerena na istraživanja populacijske strukture te tumačenje zakonitosti formiranja populacija tijekom (mikro)evolucije čovjeka, a neka su usmjerena na proučavanje značaja nasljeđa, ali i okolišnih čimbenika te njihovog složenog međudjelovanja na pojavu i progresiju fenotipskih varijacija kao što je, u ovom istraživanju, asimetrija lica koja se, kako je prije opisano, može koristiti i kao indirektna metoda u mjerenju i procjenjivanju razvojne nestabilnosti pojedine populacije.

2. SVRHA RADA

Ciljevi ovog istraživanja su:

1. Izračunati iznose totalne asimetrije cijelog kraniofacijalnog skeleta u Prokrustovim jedinicama i utvrditi grupiraju li se prema dobi.
2. Izračunati iznose totalne asimetrije cijelog kraniofacijalnog skeleta u Prokrustovim jedinicama i utvrditi grupiraju li se prema spolu.
3. Izračunati iznose totalne asimetrije kranija u Prokrustovim jedinicama i utvrditi grupiraju li se prema dobi.
4. Izračunati iznose totalne asimetrije kranija u Prokrustovim jedinicama za kranij i utvrditi grupiraju li se prema spolu.
5. Izračunati iznose totalne asimetrije mandibule u Prokrustovim jedinicama i utvrditi grupiraju li se prema dobi.
6. Izračunati iznose totalne asimetrije manidbule u Prokrustovim jedinicama i utvrditi grupiraju li se prema spolu.
7. Utvrditi totalnu asimetriju cijelog kraniofacijalnog skeleta u skupini ispitanika s područja Korčule, Visa i Splita te ima li razlike između navedenih skupina.
8. Utvrditi totalnu asimetriju za područje kranija u skupini ispitanika s područja Korčule, Visa i Splita te ima li razlike između navedenih skupina.
9. Utvrditi totalnu asimetriju za područja mandibule u skupini ispitanika s područja Korčule, Visa i Splita te ima li razlike između navedenih skupina.
10. Mijenja li se totalna asimetrija cijelog kraniofacijalnog skeleta ovisno o iznosu srođivanja.
11. Mijenja li se totalna asimetrija cijelog kraniofacijalnog skeleta ovisno o dobi.
12. Mijenja li se totalna asimetrija cijelog kraniofacijalnog skeleta ovisno o spolu.
13. Mijenja li se iznos totalne asimetrije za cijelo područje kraniofacijalnog skeleta ovisno o mjestu stanovanja (Korčula, Split, Vis).
14. Mijenja li se totalna asimetrija mandibule ovisno o iznosu srođivanja.
15. Mijenja li se totalna asimetrija mandibule ovisno o dobi.
16. Mijenja li se totalna asimetrija madnibule ovisno o spolu.
17. Mijenja li se totalna asimetrija kranija ovisno o iznosu srođivanja.
18. Mijenja li se totalna asimetrija kranija ovisno o dobi.
19. Mijenja li se totalna asimetrija kranija ovisno o spolu.
20. Usporediti iznose totalne asimetrije za cijelo kraniofacijalno područje, kranij i mandibule.

21. Utvrditi postoji li direkcijska asimetrija cijelog kraniofacijalnog skeleta u skupini ispitanika s područja Korčule, Visa i Splita te, ako postoji, ima li razlike između navedenih skupina.
22. Utvrditi postoji li direkcijska asimetrija područja kranija u skupini ispitanika s područja Korčule, Visa i Splita te, ako postoji, ima li razlike između navedenih skupina.
23. Utvrditi postoji li direkcijska asimetrija područja mandibule u skupini ispitanika s područja Korčule, Visa i Splita te, ako postoji, ima li razlike između navedenih skupina.
24. Utvrditi smjer direkcijske asimetrije i ispitati mijenja li se s obzirom na dob.
25. Utvrditi postoji li fluktuacijska asimetrija cijelog kraniofacijalnog skeleta u skupini ispitanika s područja Korčule, Visa i Splita te, ako postoji, ima li razlika između navedenih skupina.
26. Utvrditi postoji li fluktuacijska asimetrija područja kranija u skupini ispitanika s područja Korčule, Visa i Splita te, ako postoji, ima li razlike između navedenih skupina.
27. Utvrditi postoji li fluktuacijska asimetrija područja mandibule u skupini ispitanika s područja Korčule, Visa i Splita te, ako postoji, ima li razlike između navedenih skupina.
28. Mijenja li se fluktuacijska asimetrija ovisno o iznosu srođivanja.
29. Mijenja li se fluktuacijska asimetrija ovisno o dobi.
30. Mijenja li se fluktuacijska asimetrija ovisno o spolu.
31. Utvrditi smjer fluktuacijske simetrije i ispitati mijenja li se s obzirom na dob.
32. Utvrditi postojanje spolne razlike u obliku kraniofacijalnog skeleta.
33. Utvrditi postojanje dobne razlike u obliku kraniofacijalnog skeleta kod ispitanika ženskog i muškog spola.
34. Utvrditi postojanje razlike u obliku kraniofacijalnog skeleta ovisno o mjestu stanovanja ispitanika (Korčula, Split, Vis).

3. MATERIJAL I METODE

3.1. Uzorak

3.1.1. Projekt 10 001 Dalmatinac

Istraživanje se provodilo u sklopu Projekta 10 001 Dalmatinac. Projekt je dio „Croatian National Biobank“, hrvatska biobanka: Odrednice zdravlja i bolesti u općoj i izoliranim ljudskim populacijama [MZOŠ 216-1080315-0302] i *Understanding population genetics and genome-wide heterozygosity in Croatian isolated populations* [FP7 access-262055] (glavni istraživač u oba projekta je prof. dr. sc. Ozren Polašek, Medicinski fakultet Sveučilišta u Splitu).

Hrvatska biobanka je konzorcij koji povezuje više od 20 istraživačkih projekata u četiri medicinska fakulteta u Hrvatskoj, nekoliko bolnica i institucija javnog zdravstva. Koordinira ga Hrvatski centar za globalno zdravlje, na Medicinskom fakultetu Sveučilišta u Splitu. Nacionalna Biobanka oslanja se na tri velika resursa koja bi trebala osigurati i održati međunarodnu konkurentnost: 1) „10 001 Dalmatinac“ studija otočkih izolata Hrvatske; 2) banka DNA projekt baziran na analizi tisuće slučajeva s najčešćim složenim bolestima i 3) studija na velikoj skupini opće populacije u funkciji kontrolnog uzorka.

Prvi projekt međunarodno je priznata studija koja je za cilj imala provesti populacijsku studiju na 10 001 osobi s hrvatskih otoka (Visa, Lastova, Mljeta i Korčule) kako bi se njihova genetička svojstva povezala s njihovim zdravljem, bolestima i fenotipskim karakteristikama. U razdoblju od 2001. do 2007. godine studija je dobila konkurentsku potporu hrvatske Vlade, Europskog *sixth framework* programa (FP6), Velikog britanskog istraživačkog vijeća, UK *Royal Societya*, *Wellcome Trust*-a, Američkih nacionalnih instituta za zdravstvo i *British Councila*.

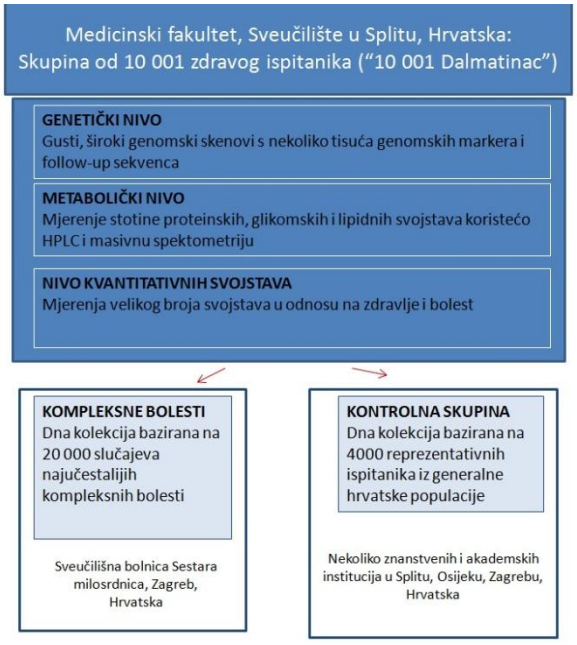
U sklopu Projekta spomenuta populacija bila je ispitana putem standardiziranog zdravstvenog upitnika, razvijenog od strane Svjetske zdravstvene organizacije, koji je uključivao dvije ankete: o općem zdravstvenom stanju i psihičkom zdravlju (140). Nadalje, poznati su osobni podaci ispitanika (dob, spol, datum rođenja), indeks tjelesne mase (*body mass index* - BMI), prehrambene navike, tjelesna aktivnost, vrijednost krvnog tlaka, omjer tlaka na rukama i nogama, nalaz elektrokardiograma, funkcija krvnih žila i pluća te gustoća kostiju. Uzeti su im uzorci krvi i urina za biokemijske i genetičke analize, testirano pamćenje, ispitan sluh i vid te su napravljene fotografije mrežnice i pregled očne pozadine (140). Na dijelu ispitanika, s područja Visa i Korčule, napravljene su CBCT snimke dijela kraniofacijalnog područja.

Drugi dio projekta baziran je na radu s bolničkim pacijentima s kroničnim bolestima. Primarno je rad baziran u Sveučilišnoj bolnici Sestara milosrdnica u Zagrebu i ima za cilj stvoriti veliku banku DNA, do 20 000 slučajeva složenih kroničnih bolesti, zaključno do 2011. godine. Kako bi se to postiglo, uključene bolnice i javno zdravstveni instituti formirali su nekoliko nacionalnih registara bolesti nepoznate etiologije i bez poznatih čimbenika rizika: amiotrofična lateralna skleroza, multipla skleroza, tip 1 šećerne bolesti, specifični rani tumori i nekoliko dječjih bolesti. Osim toga, prikupili su se i slučajevi najčešćih složenih kroničnih bolesti koji ujedno čine najveći dio ukupnog opterećenja bolesti hrvatske populacije: infarkt miokarda, moždani udar, karcinom dojke, pluća i debelog crijeva, dijabetes tipa 2, depresija, shizofrenija, bubrežni i žučni kamenci, giht, bolesti oka, Parkinsonova i Alzheimerova bolest, osteoporoza, reumatoidni artritis i drugi (113).

Zadnja studija uključuje reprezentativan uzorak od nekoliko tisuća pojedinaca iz opće hrvatske populacije koji će služiti kao kontrolna skupina za prve dvije studije. To je „ciljani uzorak“ koji usko odgovara demografskim obilježjima hrvatske populacije. Osim DNK, uzorak uključuje informacije o načinu života, navikama, izloženosti zdravstvenim rizicima, zdravstvenim stavovima i povijest bolesti koji su dokumentirane pomoću standardnih i međunarodno valjanih upitnika (140).

Glavni cilj istraživanja hrvatske nacionalne biobanke je otkrivanje prirode odnosa između: 1) genomske sekvence i sofisticiranih cirkulirajućih metabolita, 2) kružnih metabolita i kvantitativnih bioloških osobina koji su relevantni za ljudsko zdravlje i bolest i 3) kvantitativnih bioloških osobina i složene etiologije ljudske bolesti (113).

Hrvatska nacionalna biobanka u obzir uzima četiri opće razine složenosti uključene u razvoj bolesti: 1) genomsku razinu; 2) stupanj „metabolomije“ (uključujući proteomiku, glikogiju i lipidomiku); 3) razinu intermedijarnih kvantitativnih osobina (npr. krvni tlak, prisilni kapacitet ekspirija, razina kolesterola) i 4) krajnja točka koja rezultira kompleksnim fenotipom bolesti. Na svakoj razini, modifikatori poput ekoloških, kulturnih, socio-ekonomskih i psiholoških utjecaja također mogu igrati važnu ulogu.



Slika 8. Shematski prikaz svih postupaka koji su uključeni u hrvatsku biobanku (HPLC - *high performance liquid cromatography*) (preuzeto uz dozvolu iz Rudan I i suradnici, 2009) (113).

U projekt hrvatske biobanke uključeno je više od 150 hrvatskih istraživača iz različitih znanstvenih područja i disciplina koji kontinuirano traže i proširuju međunarodnu suradnju. Otkad je pokrenut, projekt je znatno povećao međunarodnu važnost i produktivnost hrvatskog biomedicinskog istraživanja u 21. stoljeću.

Biobanke su zbirke i spremišta uzoraka koje se koriste za istraživanja i u medicinske svrhe. Biobanke usmjerene na genetičku epidemiologiju trenutno dominiraju u području biomedicinskih istraživanja. Njihova veličina, ciljana populacija, shema uzorkovanja, opseg fenotipa ili bioloških uzoraka koji se prikupljaju su različiti, ali većina njih uzorkuje zdrave ispitanike koje kategoriziraju u opću ili posebnu populaciju. Jedna od posebnih populacija je izolirana otočna populacija koja zahvaljujući genetičkoj strukturi omogućuje uspješno kartiranje gena (141). Jedno od ključnih, ali često previdjelih pitanja u biobankiranju je potencijalna korist uzorkovane populacije. Postoje studije koje su identificirale razloge sudjelovanja pojedinaca u biobankingu (142, 143), ali zaključno možemo reći da su razlozi uvijek lokalno specifični i da zahtijevaju analizu od slučaja do slučaja.

Hrvatska Biobanka - 10 001 Dalmatinac primjer je izolirane populacijske biobanke, s naglaskom na genetičku osnovu složenih bolesti (130, 113). Biobanka sadrži biološke uzorke

nekoliko tisuća ispitanika s područja šest hrvatskih otoka (Vis, Korčula, Mljet, Lastovo, Rab, Susak) i obalnog grada Splita. Ovaj resurs trenutno prikuplja više od 800 fenotipskih mjerenja, uključujući uzorke krvi, seruma i urina zajedno sa sušenim krvnim mrljama (*dried blood spots*) (144), antropometrijskim i kliničkim mjerenjima, velikim brojem biokemijskih mjerenja uključujući preko 240 lipidomskih frakcija, preko 140 N-glikana, opsežne podatke o životnim navikama i kognitivnim kapacitetima. Nadalje, nedavno su započele dvije nove linije mjerenja, „senzomika“ i „antropomika“. Prvi uključuje slušne, mirisne, okusne i pragove boli, zajedno s velikim brojem percepcija i mjerenja dobivenih kompleksnim reaktinometrom Drenovac (CRD) aparat (145, 146).

Druga, „antropomika“, uključuje najsuvremenije tehnike snimanja, CBCT kraniofacijalnog skeleta i 3D skenove lica, dok se u budućnosti planira 3D skeniranje cijelog tijela.

Osim navedenog, nedavna suradnja s Hrvatskim zavodom za javno zdravstvo rezultirala je povezivanjem nacionalnih podataka o mortalitetu s podacima biobanke pružajući tako širu i sveobuhvatniju informaciju o uzrocima smrti. Biobanka će u budućnosti također pokušati povezati podatke za svakog sudionika s podacima iz zdravstvenog sustava čime bi se stvorio ažuran izvor relevantnih medicinskih informacija i napravio početni korak u razvoju integriranog okvira personalizirane medicine (147, 148, 149).

Istraživački putevi Projekta 10 001 Dalmatinac temelje se na tri linije istraživanja: 1) biologija sustava koja ima cilj razumijevanje ukupne složenosti bioloških procesa u ljudskom tijelu (150, 151), 2) analiza pleitropskih efekata i bolje razumijevanje genske mreže i 3) mogućnosti detaljnih studija udruživanja na razini fenoma s ciljem identificiranja i udruživanja velikog broja fenotipova s genima.

U sklopu druge i treće linije, ovaj je projekt istražio kako pleitropija (učinak jednog gena na više fenotipskih svojstava), genska mreža i genski putovi određuju niz klinički relevantnih kvantitativnih svojstava. Primarni fokus istraživanja je genetička osnova oblika tijela i lica, temeljenog na velikom broju mjerenja na trodimenzionalnim skenovima tijela i lica. Osim izvrsnih mogućnosti genotipizacije i sekvenciranja, uključivanje ispitanika iz izoliranih otočnih populacija olakšava otkrivanje gena i omogućuje traženje rijetkih genetičkih varijacija.

Glavni cilj Projekta bio je pridonijeti našem razumijevanju pleitropnih učinaka u našim genomima, postojanju genskih mreža i putevima gena te istražiti mogu li ih se koristiti za predviđanje kvantitativnih svojstava i pojave bolesti. Kako bi to učinili, projekt je podijeljen u pet ciljeva istraživanja, dok ovo istraživanje pripada dijelu trećeg cilja.

1) Pleitropija, mreže i putevi u određivanju oblika tijela i lica

Za ovaj cilj su se koristila antropometrijska mjerenja s ciljem: otkrivanja genetičke osnove antropometrijskih svojstava i razvijanja velike fenotip-genotipne matrice potrebne za proučavanje pleitropnih efekata, mreža i putova. Genetičke mreže i putevi istraženi su korištenjem dostupnih softverskih programa Insight i Magenta.

2) Inbreeding i oblik tijela

Ovaj projekt istražio je kako inbreeding, genske mreže i putovi identificirani u prethodnom cilju utječu na antropometrijske osobine.

3) Fluktuacijska asimetrija

Bilateralna simetrija tijela je pod genetičkom kontrolom, a genetička teorija predviđa da će povećana homozigotnost dovesti do većeg stupnja nestabilnosti genoma. To će rezultirati fenotipskim nalazom povećane fluktuirajuće asimetrije, razvojne razlike u osobinama na lijevoj ili desnoj strani tijela.

Ovaj projekt istražio je fluktuacijsku asimetriju za sve bilateralne antropometrijske i oftalmičke osobine i povezao ih s opsežnim skupom homozigotnosti na razini genoma i procjenama inbreedinga za koje se pokazalo da su veći u otočnoj populaciji (152).

4) Oblik tijela, morbiditet i smrtnost

Prethodne epidemiološke studije često su ukazivale na to da su neki oblici tijela bili povezani s povećanim rizikom od bolesti (153, 154). Ovaj projekt dodatno je razvio ovu ideju povezujući antropometrijske podatke s morbiditetom i informacijama o smrtnosti.

5) Klinički relevantne osobine

Ovaj projekt koristio je velik broj klinički relevantnih svojstava, a posebice veliku matricu lipidomskih mjera koje se sastoje od 347 mjera specifičnih lipidnih frakcija.

Projekt 10 001 Dalmatinac trebao bi nadopuniti postojeće podatke o populacijskoj genetici (137) i stvoriti sustavni i sveobuhvatni pregled genetičke strukture suvremenih Hrvata.

3.1.2. Struktura uzorka

Ukupni uzorak sadržavao je 110 ispitanika i sastojao se od triju grupa: ispitanici iz grada Splita, ispitanici s otoka Visa i ispitanici s otoka Korčule.

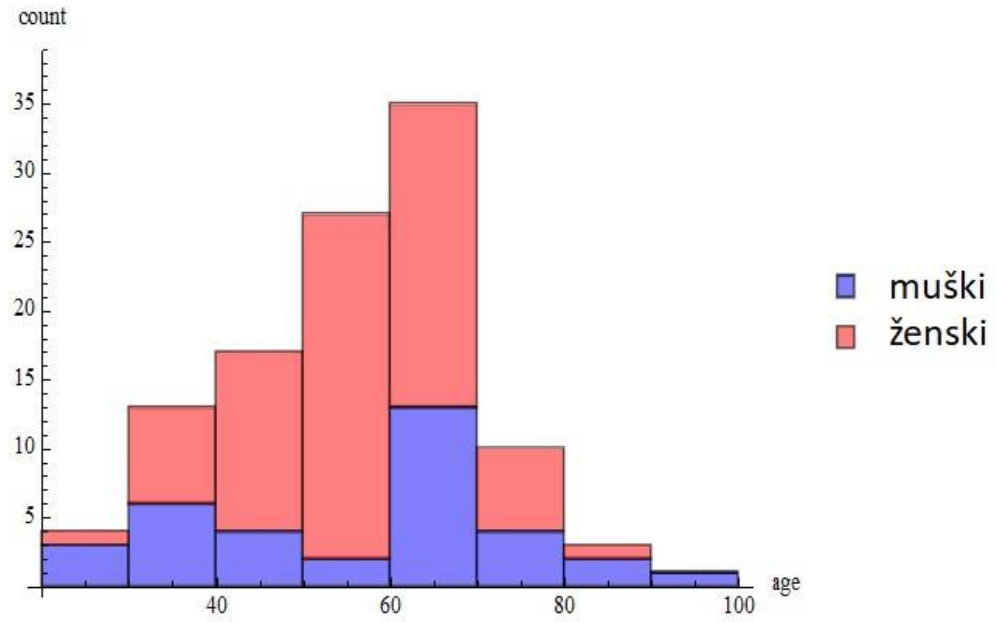
Navedena podjela učinjena ja na temelju podataka o homozigotnosti ove populacije određenu prema MLH (*mulitilocus heterozygosity*) (152) Iz grada Splita bilo je ukupno 49 ispitanika, od toga 11 muškog spola i 38 ženskog spola. S otoka Visa bilo je ukupno 46 ispitanika, od toga 20 muškog spola i 26 ženskog spola, dok je s otoka Korčule bilo ukupno 15 ispitanika, od toga 5 muškog spola i 10 ženskog spola. Spolna struktura uzorka prikazana je u **Tablici 4.**

Tablica 4. Ukupni broj i spolna struktura uzorka

Podrijetlo ispitanika	**Spol**	**Broj ispitanika**
Split		49
	ženski	38
	muški	11
Vis		46
	ženski	26
	muški	20
Korčula		15
	ženski	10
	muški	5
ukupno		110
	ženski	74
	muški	36

Struktura uzorka nije bila izabrana za potrebe ovog istraživanja, već je temeljena na dostupnim rendgenskim snimkama koje su snimane iz medicinskih razloga.

Dobna i spolna struktura cijelog uzorka prikazana je na **Slici 9**.



Slika 9. Grafički prikaz raspodjele ukupnog broja ispitanika prema dobi i spolu. Na x ordinati nalazi se dob izražena u godinama, a na y ordinati postotak ispitanika određene dobi u odnosu na ukupan uzorak. Plave kolone označavaju muški spol, a crvene kolone ženski spol. Najveći broj ispitanika odgovara dobi između 60 i 65 godina. Broj ženskih ispitanika prednjači nad muškim ispitanicima, osim u razdoblju do 20 godina i u razdoblju od 80 do 90 godina, dok su ispitanici u razdoblju od 90 do 100 godina isključivo muškog spola. Najveći broj ženskih ispitanika je u dobi između 50 i 60 godina, dok je najveći broj muških ispitanika između 60 i 70 godina.

Kao što je vidljivo, prosječna dob ukupnog uzorka iznosila je 51,3 godina, kod žena 51,1 godina, a kod muškaraca 51 godinu. U skupini grada Splita prosječna dob iznosila je 48,9 godina, kod žena 47,4 godina, a kod muškaraca 53 godine. U skupini s otoka Visa prosječna dob iznosila je 52,6 godina, kod žena 57 godina, a kod muškaraca 57 godina, dok je u skupini s otoka Korčule prosječna dob iznosila 51,8 godina, kod žena 51,4 godina, a kod muškaraca 52,8 godina.

Tablica 5. Dobna struktura uzorka

Podrijetlo ispitanika	**Spol**	**Prosječna dob ispitanika**
Split		48,9
	ženski	47,7
	muški	56
Vis		52,6
	ženski	57
	muški	49,5
Korčula		51,8
	ženski	51,4
	muški	52,8
ukupno		51,3
	ženski	51,5
	muški	51

3.2. Postupci

Mjerenja rađena u sklopu ovog istraživanja pripadaju području virtualne antropologije, novog mulidisciplinarnog područja znanosti koji podrazumijeva kvantitativnu analizu digitaliziranih anatomskih struktura u tri ili, uz komponentu vremena, u četiri dimenzije. Virtualna antropologija je realna analiza antropoloških varijacija virtualnog objekta. Ona omogućuje vizualizaciju do tada skrivenih anatomskih struktura, njihovu kvantitavnu analizu te potpuno neinvazivan pristup anatomskom mikronskom objektu interesa (ROI - *regio of interest*).

Trodimenzionalna rekonstrukcija podataka i trodimenzionalna antropometrijska mjerenja radila su se u softveru Viewbox 4 (dHAL, Greece). To je napredni program za dvodimenzionalne i trodimenzionalne kefalometrijske analize i biometrijsku morfometriju. Prvu verziju programa napravio je Halazonetis 2003. godine. i do danas je program unaprijeđen četiri puta. Zadnja verzija korištena u ovom istraživanju uključuje i trodimenzionalni modul koji omogućuje prikaz, pregled i mjerenje trodimenzionalnih anatomskih struktura. Primarna je namjena programa usmjerena na ortodontsku kliničku primjenu i znanstvena istraživanja s područja ortodoncije, dentalne medicine, medicine, biologije i virtualne antropologije.

Kako bi virtualna antropologija bila vjerodostojna analiza realnog objekta, Bookstein ju je podijelio u šest temeljnih operativnih dijelova: digitalizacija, utvrđivanje točaka, uspoređivanje, geometrijska rekonstrukcija, oblikovanje (materijalizacija) i konačna objava podataka (155).

3.2.1. Digitalizacija ili mapiranje objekta

Digitalizirati se može samo površina (virtualni šestar) ili cijeli objekt (virtualna kopija). Trodimenzionalna kopija objekta može se dobiti iz podataka snimljenih različitim uređajima: CT (kompjuterizirana tomografija), CBCT (*cone beam* kompjuterizirana tomografija), µCT (mikro kompjuterizirana tomografija), MR (magnetska rezonanca). Razlika među trodimenzionalnim kopijama dobivenih ovim uređajima je u rezoluciji, odnosno u veličini voksela.

Digitalizacija kraniofacijalnog kompleksa ispitanika ovog istraživanja rađena je CBCT uređajem. Relativno visoke doze RTG zračenja limitirale su upotrebu kompjuterizirane tomografije u orofacijalnom području samo za hitne slučajeve, kao što je tumorska dijagnostika. Upotreba CT na bazi konične zrake (CBCT) omogućila je širu primjenu u orofacijalnom području, istovremeno reducirajući dozu zračenja, povećavajući dijagnostičku vrijednost i etičku upotrebljivost. CBCT metoda bazirana je na dvije konične zrake i širokom senzoru, tako da je kut slikanja veći od 400°. Vrijeme ekspozicije značajno je reducirano upotrebom pulsne ekspozicije i analizom algoritama baziranih na širokom digitalnom zaslonu koji simultano prima slike iz svih kutova tijekom snimanja.

U ovoj fazi snimanja skupljaju se podaci mnogostrukih dvodimenzionalnih snimki za svaki pojedinačni sloj. Takav način stvaranja slike podrazumijeva da cijelo polje snimanja (FOV - *field of view*) bude registrirano iz različitih smjerova što rezultira istovremenim registriranjem velikog broja podataka, odnosno piksela za svaku točku unutar snimanog objekta. Slike koja se preklapaju, tj. duple slike dobivene iz različitih perspektiva i pozicije koriste se za kontrolu i izmjenu točnosti konačne trodimenzionalne slike.

Nakon snimanja mnoštvo prikupljenih dvodimenzionalnih snimki kompjuterski se obrađuje i analizira i u konačnici sklapa u trodimenzionalnu sliku u tri ortogonalne projekcije (aksijalna, sagitalna i koronarna), odnosno u trodimenzionalni objekt. Nakon rekonstrukcije najmanji dio snimanog objekta koji se može vizualizirati više nije piksel, nego voksel.

Ovisno o veličini i obliku detektora, moguće je mijenjati veličinu regije snimanja. Odabir veličine polja snimanja (FOV) ovisi o potrebnim specifičnim dijagnostičkim indikacijama, odnosno o regiji interesa (ROI - regio of interes).

Za ovo istraživanje koristilo se sveukupno 110 CBCT snimki. Od ukupnog broja 46 snimki pripada stanovnicima otoka Visa, 15 stanovnicima Korčule, a 49 snimaka pripada populaciji grada Splita. Sve snimke napravljene su istim CBCT uređajem (Scanora 3D, Soredex, Finland) i pripadaju bazi podataka Projekta. Ispitanici s područja otoka Visa i Korčule predstavljaju geografski i reproduktivno izoliranu populaciju, dok su se snimke ispitanika s područja grada Splita koristile kao kontrola. Ta skupina je reprezentanta miješane i neizolirane populacije. Sve su snimke istih dimenzija, veličine polja (FOV) 10 x 14,5 cm, veličine izotropnih voxela 0,25 mm sa sveukupno 300 projekcijskih snimki po ispitaniku. Snimke su pohranjene u Digital Imaging and Communication in Medicine (DICOM) formatu.

Nakon učitavanja trodimenzionalne snimke i prikaza kraniofacijalnog skeleta, određena je regija interesa za svakog ispitanika pojedinačno. Ona je uključivala cijeli kraniofacijalni kompleks, od gornjeg koštanog ruba lijeve i desne orbite te je obuhvaćala cijelu mandibulu, lateralno lijevi i desni kondilarni i koronoidni nastavak te posteriorno cijeli skelet brade. Zbog individualnih dimenzija kraniofacijalnog kompleksa, navedene strukure kod nekih ispitanika nisu bile vidljive nakon digitalizacije te su ti ispitanici izbačeni iz uzorka.

Na cijeloj definiranoj regiji interesa na histogramu je vizualizirana frekvencija i iznos denziteta sive boje za svaki pojedini voksel. Na grafu koji pokazuje krivulju vrijednosti denziteta kroz uzorak počevši od najniže vrijednosti, uzlazne putanje pa sve do najviše vrijednosti denziteta po principu prozoriranja odredila se srednja vrijednost denziteta. Izgled grafa, odnosno nagib uzlazne putanje ovisi o homogeniziranosti koštanog tkiva svakog ispitanika i individualan je. Isto tako je i širina prozora koji obuhvaća početak i završetak uzlaznog kraka različita. Sve tkivo koje je po iznosu HU bilo izvan prozora izbačeno je i na njemu nisu rađena mjerenja. Postupak „prozoriranja“ čisti uzorak i povećava njegovu homogenost.

Drugi postupak kojim se povećala homogenost površine koštanog tkiva je zaglađivanje površine. Ono uključuje niz programskih geometrijskih, perceptivnih i transformirajućih promjena kojima se površina tkiva izoštrava te detalji postaju bolje vidljivi.

3.2.2. Utvrđivanje antropometrijskih točaka

Drugi operativni proces koji slijedi nakon digitalizacije pripremljenog i „očišćenog“ virtualnog modela je definiranje i određivanje položaja pojedinačne točke u sve tri ravnine (transverzalnoj, sagitalnoj i konorarnoj) kao i na trodimenzionalnoj rekontrukciji.

Osnovni preduvjet upotrebe postupaka geometrijske morfometrije je digitalizacija antropometrijskih točaka za sve objekte ispitivanja. Digitalizacija točaka u sve tri dimenzije znantno je kompleksnija nego u dvije gdje se točke označavaju putem računala na fotografiji ili rendgenogramu.

Prema Booksteinu, moguće je definirati 3 tipa krivulja (vidljive, najizraženije, simetrične) i 6 tipa točaka (najuočljivije - određene sjecištem triju dijelova tkiva u prostoru, najuočljivije izbočine anatomske strukture, točke određene simetrijom - sjecište grebena i medijalne linije,

nauočljivije krivine i medijalne linije ili sjecište grebena i najuočljivije krivine, polutočke krivulje, polutočke površine i kontrukcijske polutočke) (155).

Promatranje bioloških struktura provodi se pomoću podataka koje čine koordinate točaka u dvije ili u tri dimenzije. U tu svrhu mogu se koristiti antropometrijske točke (*landmarks*) i točke izvan objekta (*outline coordinates*). Antropometrijske točke su specifične točke organizma koje odgovaraju promatranom objektu i one su u većoj ili manjoj mjeri homologne, za razliku od točki izvan objekta koje nisu homologne. Homolognost je bitan preduvjet u definiranju antropometrijskih točaka i taj se termin koristi u svrhu opisivanja identičnih dijelova oblika organizma kod različitih vrsta ili razvojnih stadija, odnosno bioloških struktura koje imaju stalno, odnosno identično biološko ili biomehaničko značenje (156).

Postoje tri osnova tipa antropometrijskih točaka:

1) Tip I su točke koje se najlakše identificiraju, a njihova je homolognost čvrsto dokaziva i biološki utemeljena. One su unutar uzorka potpuno homologne, ponovljive su i vrlo dobro vidljive na promatranoj strukturi pa su najvrjedniji podaci za analizu geometrijskom morfometrijom. To su obično vrhovi grebena, sjecista sutura, prelazi jednog tkiva u drugi itd.

2) Tip II su točke čija je homolognost uvrđena geometrijskim pristupom, a najbolji primjer za to su najoštrije krivulje zuba.

3) Tip III su točke kojima nedostaje barem jedna koordinata. Primjer za to je točka dna konkaviteta na dvodimenzionaloj slici. One se koriste u statističkoj obradi, ali u biološkoj i geometrijskoj interpretaciji treba ih uzimati s oprezom. Ukoliko se homolognost ne može utvrditi koriste se pseudo-točke (*pseudo-landmarks*) koje se najčešće nalaze na početku ili kraju proučavane strukture, na najizbočenijem dijelu krivulje ili proizvoljno izvan strukture objekta (156).

Točke tipa I odgovaraju Mossovim „materijalnim“ točkama, a točke tipa II i III odgovaraju „anatomskim“ točkama. Anatomske kranijalne točke mogu biti dvojake: točke koje se nalaze na površini kosti (gonion, mention, spina nasalis anterior) što bi otprilike odgovaralo točkama tipa II i točke koje se nalaze između dviju točaka (nasion, bregma), odnosno Booksteinove točke tipa III. Ukoliko rast teče uniformno kroz sva tkiva, možemo očekivati da se materijalne i anatomske točke pomiču zajedno, poput procesa koji se odvija tijekom intersticijskog rasta.

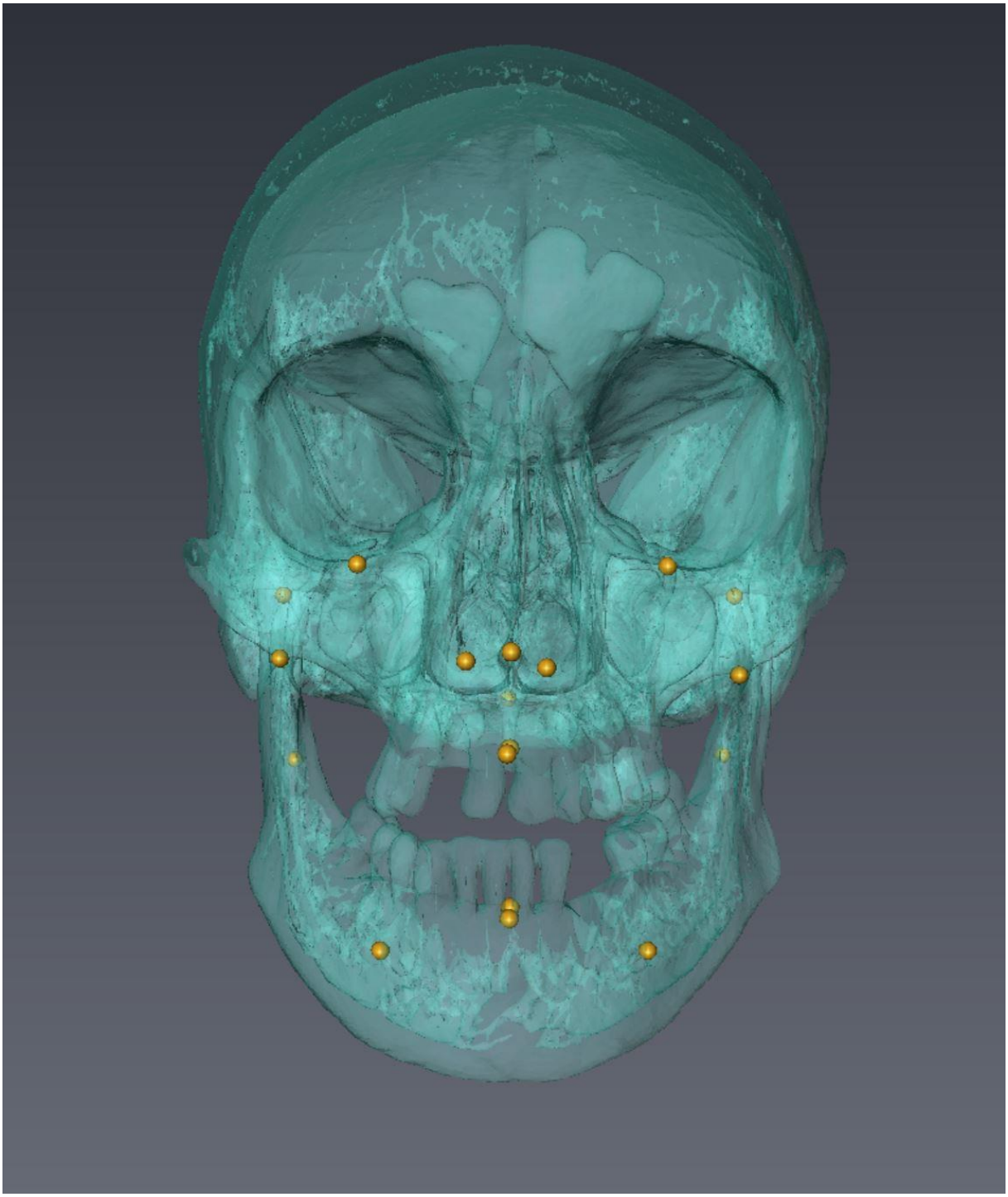
Na dijelu kraniofacijalnog skleleta od donjeg ruba orbite do donjeg ruba mandibule nalazi se 6 neparnih kraniometrijskih točaka u mediosagitalnoj ravnini i 14 parnih točaka.

Točke u mediosagitalnoj ravnini koje će se koristiti su: prosthion (pr), spina nasalis anterior (sna), spina nasalis posterior (snp), foramen incisivus (fi), linguale (lng) i infradentale (id). Parnim točkama pripadaju: orbitale (or), apertura piriformis (ap), zygoorbitale (zo), zygomaxillare (zm), foramen mandibule (fma), foramen mentale (fme) i coronoid (cn). Njihove definicije (157) navedene su u **Tablici 6,** a prostorni položaj prikazan je na **Slikama 10 i 11**).

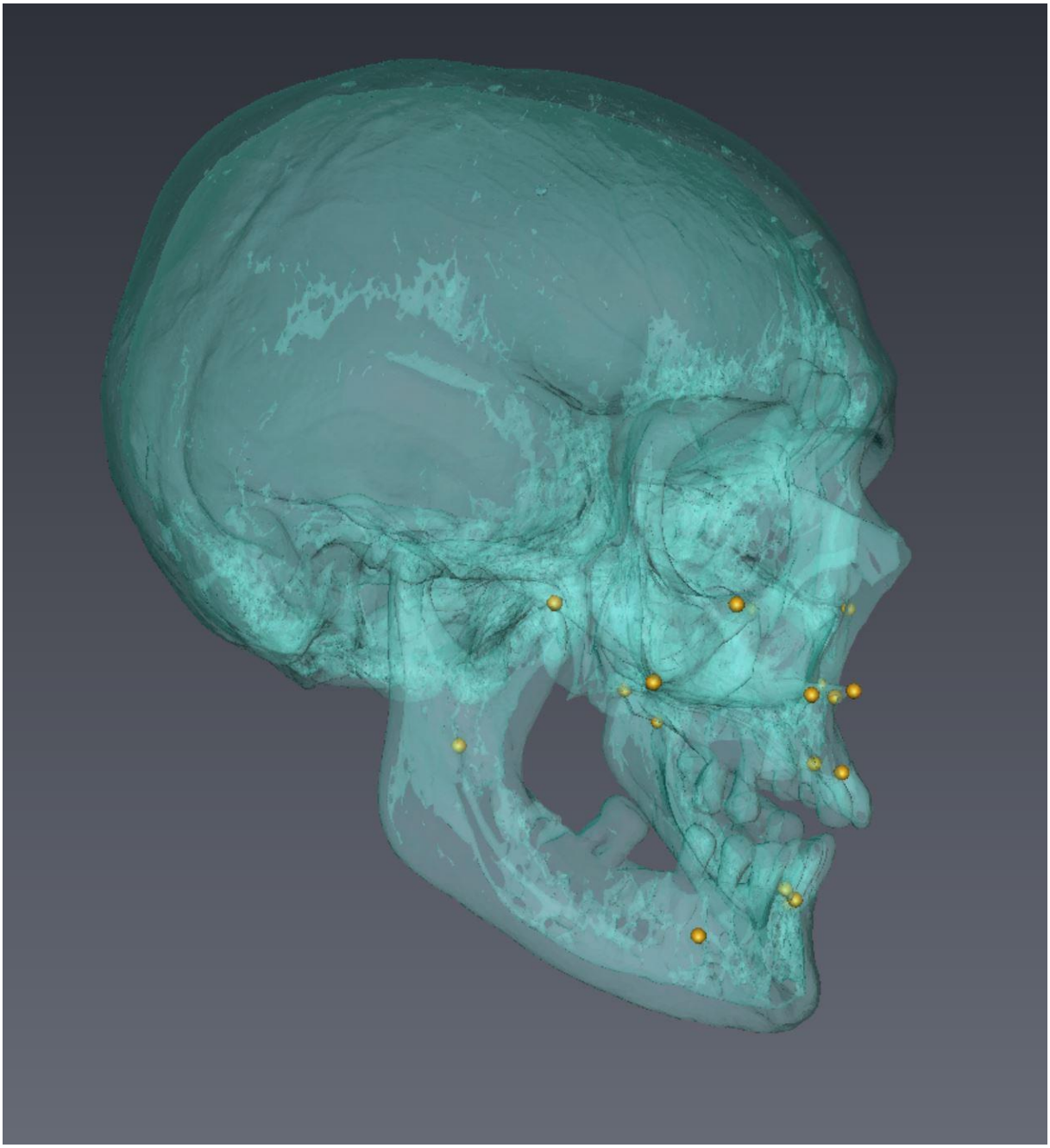
Tablica 6. Definicije točaka (preuzeto uz dozvolu iz Muretić Z i suradnici, 2014.) (157).

Ime antropometrijske točke	**Definicija i položaj**
neparne točke	
prosthion (pr)	najanteriornija i najinferiornija točka maksilarnog alveolarnog nastavka, najčešće se nalazi u blizini caklinskog-cementnog spojišta maksilarnih centralnih inciziva
spina nasalis anterior (sna)	najanteriornija točka dna nosne šupljine, vrh premaksile i mediosagitalnoj ravnini
spina nasalis posterior (snp)	točka sjecišta tvrdog i mekog nepca i fose pterigopalatine
foramen incisivus (fi)	središnja točka incizalnog kanala, najčešće se nalazi između kruna centralnih maksilarnih inciziva
linguale (lng)	najanteriornija i najsuperiornija točka mandibularnog alveolarnog nastavka, najčešće se nalazi blizu caklinsko-cementnog spojišta mandibularnih centralnih inciziva s lingvalne strane
infradentale (id)	najanteriornija i najsuperiornija točka mandibularnog alveolarnog nastavka, obično se nalazi u blizini caklinsko - cementskog spojišta mandibularnih centralnih inciziva s vestibularna strane
parne točke	
apertura piriformis (ap)	najinferiornija točka suture gdje maksila artikulira s

	nazalnim kostima
zygoorbitale (zo)	najsuperionija točka zigomatičnog luka
zygomaxillare (zm)	najinferiornija točka zigomatičnog luka
foramen mandibule (fma)	središnja točka vanjskog ruba foramena mandibule
foramen mentale (fme)	središnja točka vanjskog ruba foramena mentale
coronoid (cn)	najsuperiornija točka koronoidnog nastavka



Slika 10. Položaj antropometrijskih točaka – frontalni pogled (Slika pokazuje položaj antropometrijskih točaka u frontalnom pogledu. Vide se: zygoorbitale desno, zygoorbitale lijevo, apertura piriformis desno, apertura piriformis lijevo, spina nasalis anterior, coronoid desno, coronoid lijevo, prosthion, linguale, infradentale, foramen mentale desno, foramen mentale lijevo.



Slika 11. Položaj antropometrijskih točaka - lateralni pogled (Slika pokazuje položaj antropometrijskih točaka lateralno. Vide se: zygoorbitale desno, zygomaxillare desno, apertura piriformis desno, spina nasalis anterior, prosthion i foramen mentale desno.)

Lubanja koja se koristi za vizualizaciju dobivena je ljubaznošću od dr. Lynn Copes. Ona je dio zbirke od preko 700 CT skenova ljudskih lubanja i 400 microCT skenova lubanja nehumanih primata (https://www.lynncopes.com/human-ct-scans.html).

Cjelokupna lubanja svakog pojedinca skenirana je Siemens Somatomovim spiralnim skenerom (70 µA, 110 kV, visina stola 215, širina rezova 1,0 mm, rekonstrukcija 0,5 mm - najveća moguća rezolucija na skeneru u vrijeme skeniranja). Uzorci su morali biti skenirani u dva dijela kako bi se skener mogao ohladiti na polovini skeniranja. Prikazana lubanja potječe iz zbirke Terry, zbirke iz SAD-a. Njena oznaka je TC 880.

Sporedna datoteka kaže da je lubanja iz ženske osobe od 27 godina, visine 175 cm, rođene 1904., a umrle od kroničnog nefritisa 5. veljače 1931. godine.

Nakon digitalizacije, antropometrijske točke određene su svojim koordinatama (x, y, z) i analizirane su metodama geometrijske morfometrije u programu Mathematica 4.1 (Wolfram Research, Inc., United Kingdom).

3.2.3. Analize metodama geometrijske morfometrije

Morfometrija obuhvaća metode opisa i statističke obrade varijacija oblika unutar uzorka i među uzorcima, analize promjena oblika uslijed rasta i razvoja, primjene eksperimentalnih metoda i praćenje evolucijskih promjena antropometrijskih obilježja čovjeka i njegovih predaka (158). Ona se može koristiti kada je potrebno opisati oblik dijela organizma ili određenu strukturu te usporediti različite ili slične oblike.

Multivarijantna ili tradicionalna morfometrija karakterizirana je uporabom multivarijantnih statističkih postupaka nad određenim grupama varijabli. Kao antropometrijske varijable najčešće se koriste udaljenosti između pojedinih antropometrijskih točaka (*landmarks*) ili struktura organizma. Tako se utvrđuju različite duljine i širine te njihovi međusobni omjeri. U tradicionalnoj morfometriji mjere se i određeni kutovi i razmjeri. Rezultati se pokazuju brojčano i grafički ukazujući na ovisnost dviju ili više varijabli.

Jedan od problema tradicionalne morfometrije nalazi se u činjenici da čak i u slučaju velikog broja utvrđenih mjera lica nije moguće vizualizirati njegov oblik. Također, više promatranih mjera organizma mogu imati zajedničku antropometrijsku točku što se u multivarijantnoj analizi ne obrađuje pa stoga rezultati nisu toliko vjerodostojni kao što bi bili da se ne

obrađuje. Prikaz rezultata u obliku udaljenosti težak je za vizualizaciju promjena samog oblika organizma.

Geometrijska morfometrija je morfometrijski pristup koji čuva geometriju određenog oblika. Između nekoliko geometrijskih pristupa, Prokrustova metoda je najraširenija i najlakše razumljiva u svojim matematičkim i statističkim svojstvima (159).

Geometrijska morfometrija je skup postupaka multivarijantnih statističkih analiza antropometrijskih točaka u kartezijskom koordinatnom sustavu. Riječ „geometrijska“ odnosi se na Kendellov *shape-space*, odnosno na procjenu prosječnog oblika i opis varijacije oblika unutar uzorka (160). U tom prostoru svaka točka predstavlja oblik unutar nekog euklidskog prostora (161). Većina multivarijantnih metoda predstavlja linearizaciju statističkih analiza udaljenosti između točaka i orijentacije točaka unutar prostora. Multivarijantnost u geometrijskoj morfometriji koristi se u procjeni izgleda prosječnog oblika na razini cijelog uzorka. Osnovna je značajka očuvanje svih podataka u relativnom razmještaju svim promatranih točaka jer se tijekom analize analiziraju sve točke zajedno (162). Tako je moguće vizualizirati varijabilnost pojedinca ili promatrane grupe unutar uzorka i u odnosu na cijeli uzorak te varijacija cijelog uzorka u odnosu na pojedinca ili na promatranu skupinu unutar njega. U tradicionalnoj morfometriji potrebno je već unaprijed odrediti udaljenosti koje će se mjeriti, a za koje se pretpostavlja da u određenoj mjeri odražavaju poremećaj oblika. Za razliku od toga u geometrijskoj morfometriji sama analiza ukazuje na smjer maksimalne varijance i objašnjava koja je varijabla najznačajnija za određenu prostornu promjenu (160).

Za analizu oblika i simetrije kraniofacijalnog skeleta koristit će se sljedeće metode: opća Prokrustova metoda superpozicije kojom će se standardizirati veličina objekta i maknuti iz analize faktor veličine promatranog objekta, modeliranje preslike objekta te metoda glavnih komponenata (*Principal Components Analysis* - PCA) (163).

3.2.3.1. Standardiziranje veličine objekta (Opća Prokustova metoda superpozicije)

Standardiziranje veličine objekta provodi se u svrhu micanja čimbenika veličine kako bi u predstojećim analizama preostao samo čimbenik oblika kao predmet analize. Standardiziranje veličine objekta u geometrijskoj morfometriji provodi se korištenjem Prokrustove analize. Postoje dva oblika Prokrustove analize: jednostavna i opća. Jednostavnom se određuje centroidna veličine (*centroid size*), odnosno prosječna točka uzorka s koordinatama (0, 0, 0).

Općom Prokrustovom metodom superpozicije, koja postavlja svaki objekt prema svakome, utvrđuje se srednja vrijednost uzorka. Ona se računa programima koji odabiru koordinatu x, sve koordinate prilagođavaju toj koordinati, utvrđuju sumu kvadrata razlika, izračunavaju novu srednju vrijednost i taj se postupak višestruko ponavlja do vrijednosti do oko 10^{-6}. Tom metodom minimiziranja sume kvadrata odstupanja svih antropometrijskih točaka odredio se Prokrustov prosječni oblik i Prokrustove koordinate u odnosu na prosječni oblik.

Pri refleksiji i preslikavanju svaka se koordinata (x, y, z) preslika pa tako i Prokrustov prosječni oblik. Stoga ga još možemo nazvati simetričnim prosječnim oblikom originalnog oblika.

3.2.3.2. Modeliranje preslike objekta i stvaranje simetričnog objekta

Modeliranje preslike objekta omogućava stvaranje refleksije lijeve i desne strane objekta. Matematički postupci utvrđivanja ukupne asimetrije provedeni su prema Mardia (50). Prema njima, simetrija bioloških objekata, tkiva ili sustava može se podijeliti u dvije grupe. Prvoj grupi (*object symmetry*) pripadaju parametri neparnih obilježja koji se nalaze u mediosagitalnoj ravnini, dok su u drugoj grupi (*matching symmetry*) pripadaju parametri parnih obilježja koji se nalaze lateralno lijevo i desno od mediosagitalne ravnine. Unutar prve grupe postoje dvije vrste antropometrijskih točaka - uparene, koje nisu na mediosagitalnoj ravnini već lateralno od nje i neuparene koje su točno na mediosagitalnoj ravnini.

Matematički opis oblika nekog objekta predstavlja grupu antropometrijskih točaka (*landmarks*) koji ga definiraju, standardizirani s obzirom na vektorske karakteristike, tj. na lokaciju, vrijednost i smjer.

Krajnji rezultat postupaka refleksije u mediosagitalnoj ravnini i preslikavanja permutacijskom matricom je prostorno nepromijenjen međusobni odnos koordinata antropometrijskih točaka

unutar jednog objekta. Dobiva se njegova identična zrcalna preslika koja je identična originalnom obliku.

Preslikavanje objekta kod dvodimenzionalnih točaka odvija se preko mediosagitalne ravnine, a kod trodimenzionalnih točaka oko mediosagitalne plohe. Mediosagitalna linija ili ploha zamišljena je linija ili ploha koja prolazi kroz sredinu tijela i dijeli organizam na dva dijela. Budući da je sredina tijela određena antropometrijskim točkama, a njihova je pozicija varijabilna, mediosagitalnu ravninu na takav način nije moguće točno odrediti. Za točno određivanje simetričnosti objekta zbog toga se koristi gore navedeni matematički model inverzije i preslikavanja te je na taj način izbjegnuta pogreška određivanja pozicije mediosagitalne ravnine.

Modeliranjem preslike objekta stvorili su se preduvjeti za utvrđivanje ukupne asimetrije. Stupanj individualne morfološke asimetrije izračunao se kao razlika oblika (Prokrustova udaljenost) između konfiguracije lica i njegove zrcalne refleksije.

3.2.3.3. Izračun devijacija od simetričnog objekta i statistička obrada asimetrije

Postupci utvrđivanja direkcijske i fluktuacijske asimetrije temelje se na postupku dekompozicije ukupne asimetrije. Prvoutvrđena ukupna asimetrija (totalna asimetrija - TA) uzorka podijeljena je na direkcijsku (direkcijska asimetrija - DA) i fluktuacijsku asimetriju (fluktuacijska asimetrija - FA).

Ukupna asimetrija je ukupna suma kvadrata razlika udaljenosti između originalnog objekta i njegove određene preslike. Direkcijska ili međugrupna asimetrija je razlika između grupe koja predstavlja promatrani objekt i grupe koja opisuje srednju vrijednost (suma kvadrata razlike objekta u odnosu na srednju vrijednost). Fluktuacijska asimetrija predstavlja razliku unutar grupne asimetrije što označava iznos do kojeg uzorak fluktuira oko srednje vrijednosti.

Metoda glavnih komponenata (*Principal Components Analysis*, PCA) ukazala je na distribuciju dominantnih varijacija oblika unutar različitih populacija i prikazala glavne različitosti među njima (43).

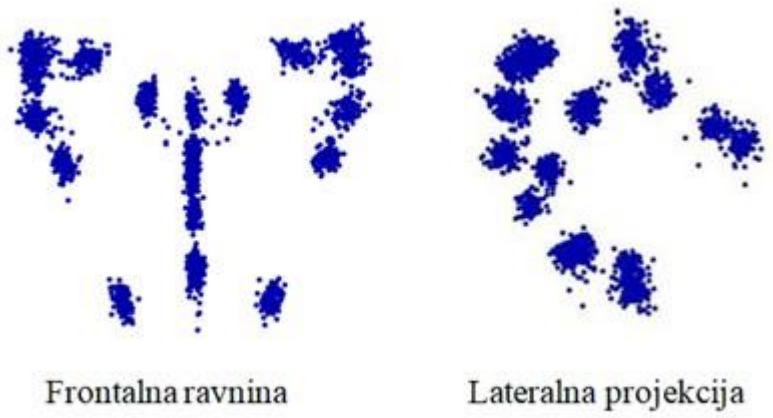
4. REZULTATI

U prvom dijelu ovog poglavlja prikazat će se rezultati analize oblika kraniofacijalnog skeleta metodom geometrijske morfometrije, nakon što je općom Prokrustovom analizom maknut faktor veličine. Pokazat će se promjena oblika u odnosu na dob te distribucija oblika kraniofacijalnog skeleta između spolova.

Drugi dio ovog poglavlja pokazat će rezultate analize asimetrije kraniofacijalnog skeleta nakon modeliranja preslike objekta i stvaranja simetričnog. Prikazat će se i distribucija totalne asimetrije na razini cijelog uzorka, rezultati analize totalne asimetrije prema mjestu stanovanja te rezultati direkcijske i fluktuacijske asimetrije.

4.1. Rezultati standardizacije veličine objekta

Standardizacija veličine objekta provedena je korištenjem opće Prokrustove analize. Nakon digitalizacije, sve parne i neparne antropometrijske točke su superponirane.

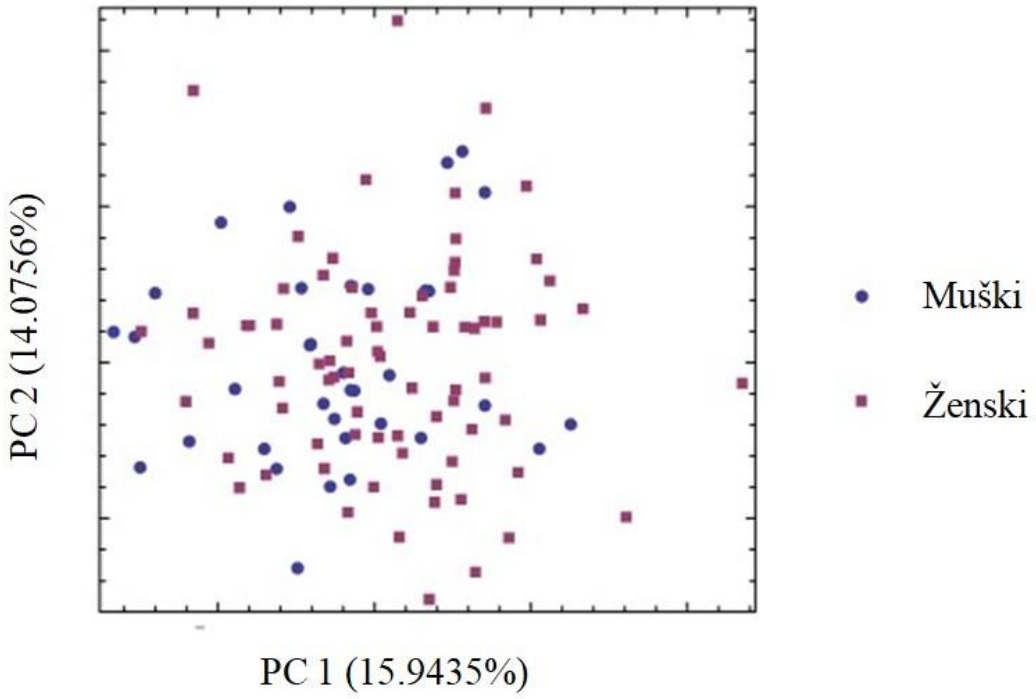


Slika 12. Prokrustove koordinate čitavog uzorka

Slika 12. prikazuje Prokrustove koordinate čitavog uzorka, odnosno rezultate standardizacije veličine objekta. Lijevi dio slike prikazuje antropometrijske točke u frontalnoj ravnini, dok desni dio slike prikazuje antropometrijske točke u lateralnoj projekciji. Temeljem slike može se zaključiti kako se radi o homogenom uzorku budući da su sve antropometrijske točke čitavog uzorka ravnomjerno raspoređene. Osim toga, dobiven je raspored antropometrijskih točaka uz isključenje čimbenika veličine objekta tako da je preostala samo varijabilnost oblika.

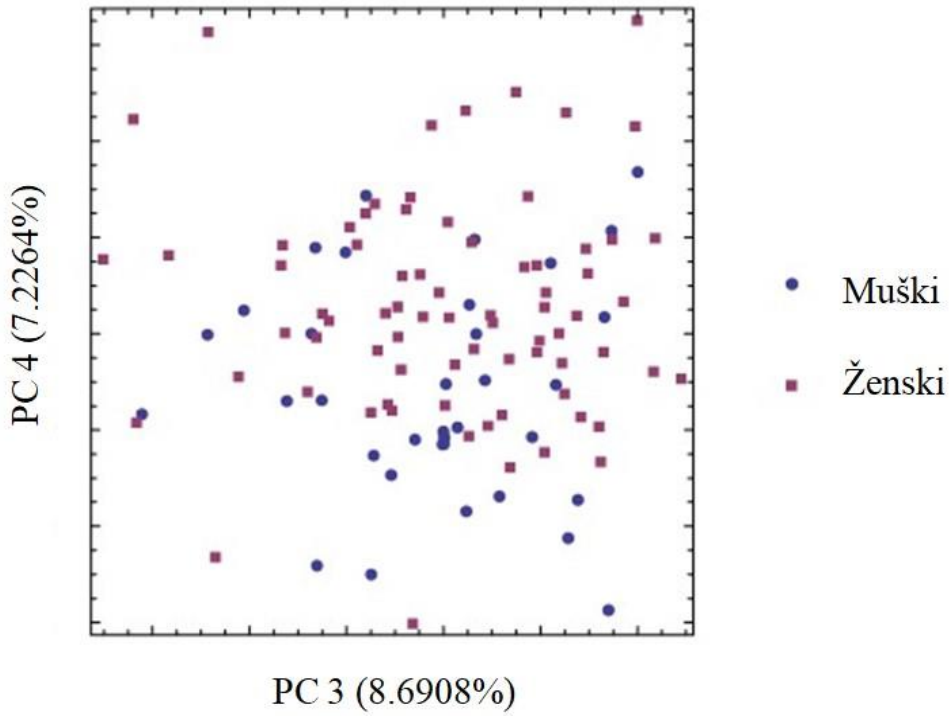
4.2. Rezultati analiza oblika kraniofacijalnog skeleta

4.2.1. Rezultati distribucije oblika kraniofacijalnog skeleta između spolova



Slika 13. Prva i druga glavna komponenta distribucije oblika kraniofacijalnog skeleta između spolova

Slika 13. prikazuje prvu i drugu glavnu komponentu distribucije oblika kraniofacijalnog skeleta između spolova. Na ordinati su grafički prikazane vrijednosti prve glavne komponente, a na apsici vrijednosti druge glavne komponente za svakog ispitanika. Ispitanici označeni plavim krugom pripadaju muškom spolu, a ispitanici označeni ljubičastim kvadratom pripadaju ženskom spolu. Kao što se može vidjeti na slici, ispitanici se prema spolu ne grupiraju u klastere.

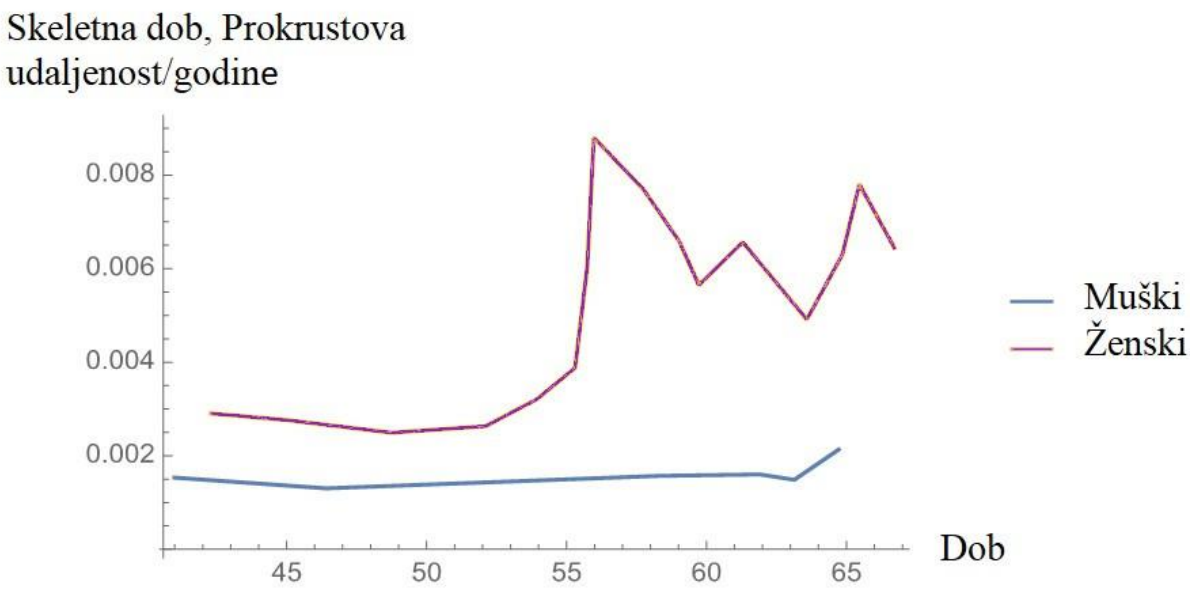


Slika 14. Treća i četvrta glavna komponenta distribucije oblika kraniofacijalnog skeleta između spolova

Slika 14. prikazuje treću i četvrtu glavnu komponentu distribucije oblika kraniofacijalnog skeleta između spolova. Na ordinati su grafički prikazane vrijednosti treće glavne komponente, a na apsici vrijednosti četvrte glavne komponente za svakog ispitanika. Ispitanici označeni plavim krugom pripadaju muškom spolu, a ispitanici označeni ljubičastim kvadratom pripadaju ženskom spolu. Kao što se može na vidjeti na slici, ispitanici se prema spolu ne grupiraju u klastere.

Iako vidimo da između ispitanika ženskog i muškog spola postoje mnoga preklapanja i nema vidljivog grupiranja, F test pokazao je da između ispitanika ženskog i muškog spola postoji statistički značajna razlika oblika kraniofacijalnog skeleta (p=0.025).

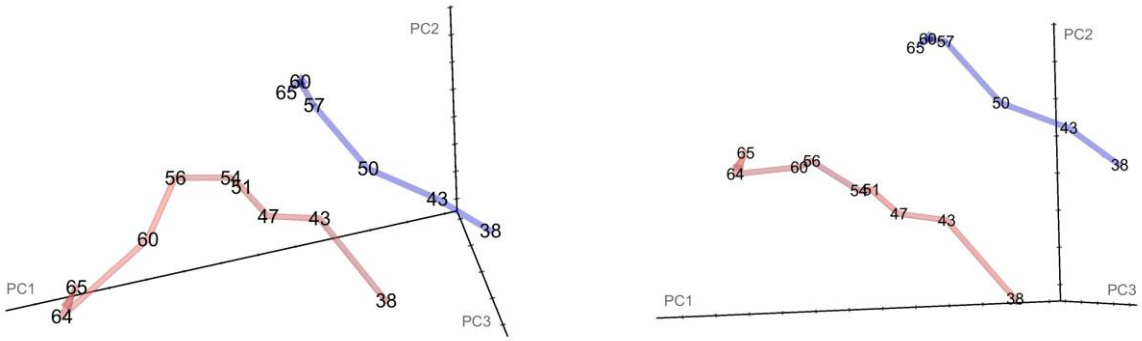
4.2.2 Rezultati analize promjena oblika kraniofacijalnog skeleta u odnosu na dob



Slika 15. Ovisnost promjene oblika kraniofacijalnog skeleta u odnosu na dob kod ispitanika muškog i ženskog spola

Slika 15. pokazuje ovisnost promjene oblika kraniofacijalnog skeleta u odnosu na dob kod ispitanika muškog i ženskog spola. Na x osi prikazana je dob ispitanika izražena u godinama. Na y osi prikazana je skeletna dob koja je izražena u jedinici Prokrustove udaljenosti u godini dana. Ta jedinica označava promjenu oblika kraniofacijalog skeleta koja se dogodi u godini dana. Dobivena je na način da je u svrhu analize oblika maknut faktor veličine glave, nakon čega je svaki ispitanik dobio svoj broj PD jedinica (*Procrust distance* - Prokrustova udaljenost) koje označavaju promjenu oblika.

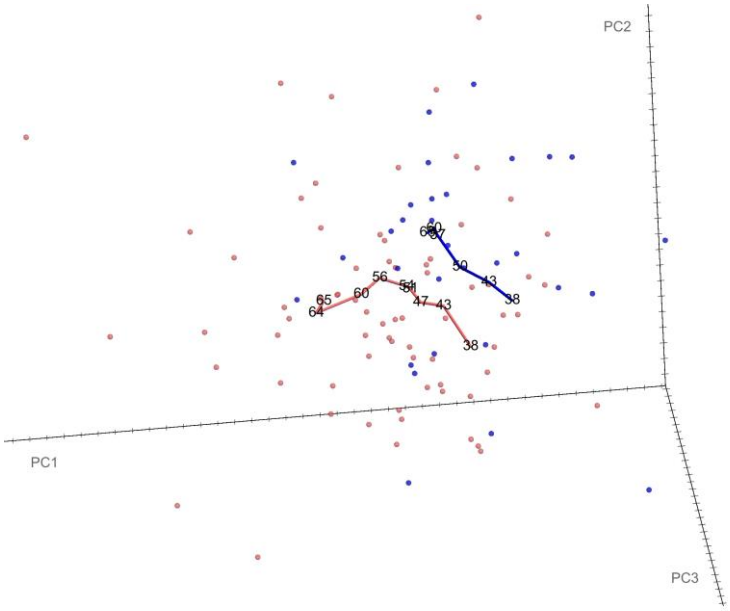
Vidimo da se krivulje ispitanika muškog i ženskog spola razlikuju. Promjene oblika kraniofacijalnog skeleta veće su kod ispitanika ženskog, nego kod ispitanika muškog spola. Nakon 55 godina krivulja promjene oblika kraniofacijalnog skeleta u ovisnosti o dobi kod ispitanika ženskog spola ima izraženu uzlaznu putanju nakon čega postaje diskontinuirana s nepredvidljivim uzlaznim i silaznim varijacijama.



Slika 16. Prosječni oblik glave svih ispitanika u ovisnosti o dobi i spolu

Slika 16. prikazuje prosječni oblik glave svih ispitanika vezan uz dob, procijenjen lokalnim linearnim regresijama, ovdje je prikazan PC1, PC2 i PC3. Plava krivulja označava promjene glave u odnosu na dob (izraženu u godinama) kod muškarca, dok crvena krivulja označava promjene glave u odnosu na dob (izraženu u godinama) kod žena.

Putanje krivulja muškaraca i žena približno su paralelne do otprilike 55 godine kada se kod žena mijenja obrazac starenja i promjene oblika kraniofacijalnog skeleta uzrokovane starenjem. Putanja krivulje muškarca konstantno je uzlaznog tijeka i ne mijenja se.



Slika 17. Promjene oblika kraniofacijalnog skeleta ispitanika ženskog i muškog spola

Slika 17. prikazuje promjene oblika kraniofacijalnog skeleta u odnosu na dob kod ženske i muške populacije ispitanika. Vide se izražene pojedinačne varijacije oko prosječnih uzoraka i za žensku i za mušku populaciju.

Tablica 7. Promjene oblika kraniofacijalnog skeleta kod ispitanika muškog i ženskog spola u ovisnosti o dobi

Promjene oblika kraniofacijalnog skeleta kod ispitanika ženskog i muškog spola u ovisnosti o dobi			
CIJELI UZORAK	MLAĐI OD 55 GODINA	STARIJI OD 55 GODINA	STARIJI OD 49.3. GODINA
p=0.008	*p*=0.002	*p*=0.52	*p*=0.067

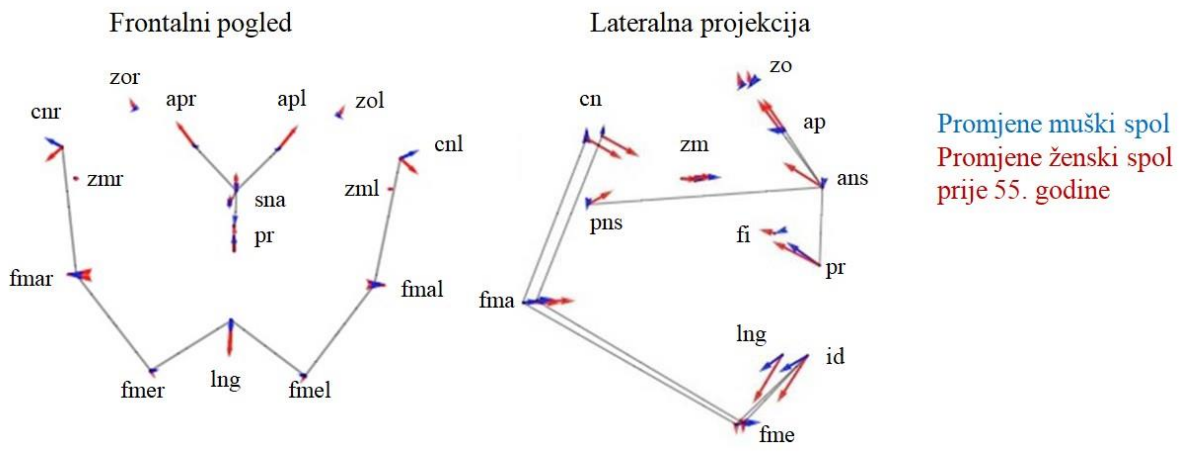
Tablica 7. pokazuje da između ispitanika muškog i ženskog spola postoji statistički značajna razlika u promjenama kraniofacijalnog skeleta koje se događaju ovisno o dobi (*p*=0.008). Između ispitanika muškog spola i ženskog spola mlađih od 55 godina postoji statistički značajna razlika u promjenama kraniofacijalnog skeleta koje se događaju ovisno o dobi (*p*=0.002), dok između ispitanika muškog spola i ženskog spola starijih od 55 godina ne

postoji statistički značajna razlika u promjenama oblika kraniofacijalnog skeleta koje se događaju ovisno o dobi (p=0.52).

U sklopu Projekta ispitanici ženskog spola su putem upitnika odgovorili na pitanja o vremenu zadnje menstruacije i trajanju postmenopauznog razdoblja. Na temelju toga izračunano je prosječno vrijeme menopauze kod ispitanika ženske populacije ovog uzorka koje odgovara razdoblju iza 49.3 godina. Od ukupnog broja ispitanika ženskog spola, njih 32 starije je od prosječnog vremena nastupanja menopauze (49.3 godina). Između ispitanika ženskog spola starijeg od 49.3. godina i muškog spola ne postoji statistički značajna razlika u promjenama oblika kraniofacijalnog skeleta koje se događaju ovisno o dobi (p=0.067).

4.2.3. Rezultati analiza promjena oblika kraniofacijalnog skeleta kod oba spola u periodu oko i nakon menopauze kod žena

S obzirom na navedene rezultate, uzorak ispitanika ženskog spola analiziran je u dobi prije 55. godine i nakon 49.3 godine (prosječno vrijeme nastupanja menopauze) kada dolazi do intenzivnih promjena oblika kraniofacijalnog skeleta.



Slika 18. Vektorski prikaz promjene oblika kraniofacijalnog skeleta kod ispitanika ženskog i muškog spola mlađih od 55 godina

Slika 18. pokazuje promjene oblika kraniofacijalnog skeleta kod ispitanika ženskog i muškog spola mlađih od 55 godina u vektorskom obliku. Crveni vektori označavaju promjene oblika kraniofacijalnog skeleta kod ispitanika ženskog spola, dok plavi vektori označavaju promjene oblika kraniofacijalnog skeleta kod ispitanika muškog spola. Na slici se može zamijetiti da su vektori crvene boje dulji od plavih, što označava da su promjene oblika kraniofacijalnog skeleta kod ispitanika ženskog spola intenzivnije od promjena kod ispitanika muškog spola. Za razliku od intenziteta, smjerovi crvenih i plavih vektora su slični što dovodi do zaključka da su i smjerovi oblika promjena kraniofacijalnog skeleta u odnosu na dob kod ispitanika muškog i ženskog spola slični.

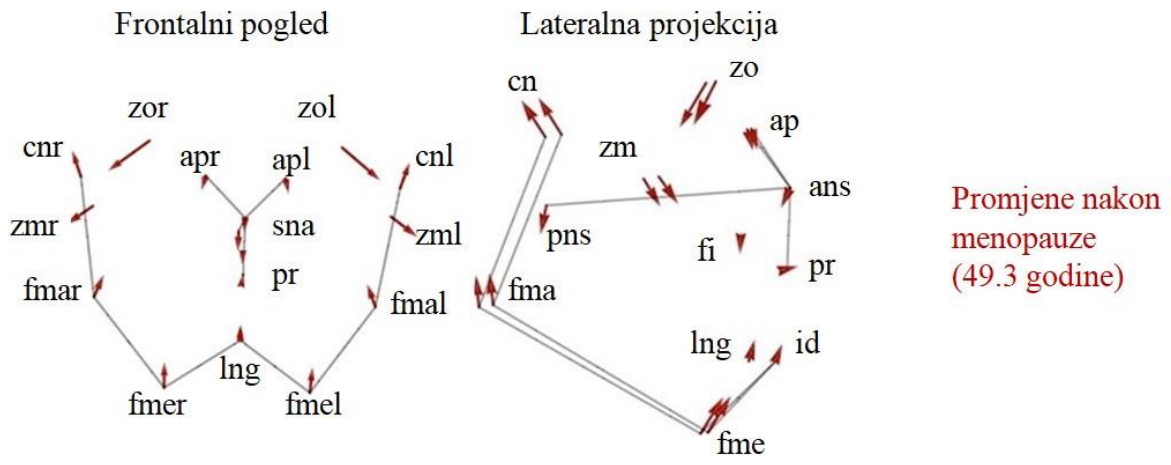
Gotovo neznatne i najmanje promjene vide se na točkama: zygoorbitale desno (zor) i lijevo (zol), zygomaxillare desno (zmr) i lijevo (zml), foramen mandibule desno (fmar) i lijevo (fmal) foramen mentale desno (fmer) i lijevo (fmel) te foramen incizivus (fi). Promjene su najizraženije na točkama: apertura piriformis desno (apr) i lijevo (apl), coronoid desno (cnr) i

lijevo (cnl), anteriorna nazalna spina (ans), posteriorna nazalna spina (pns), linguale (lng), infradentale (id), te prostion (pr).

Promjene točke apertura piriformis uzrokovane porastom dobi intenzivnije su kod ispitanika ženskog spola i usmjerene su kraniolateralno.. Točka infadentale i linguale kod ispitanika ženskog i muškog spola spola pomiče se prema kaudalno, dok se točka prostion pomiče kranijalno.

U lateralnom pregledu vidi se da su promjene točke coronoid s porastom dobi događaju samo kod ispitanika ženskog spola i usmjerene su kaudomedijalno pod kutem od oko 60 stupnjeva.

Promjene točke spina nasalis anterior i spina nasalis posterior uzrokovane porastom dobi također se događaju samo kod ispitanika ženskog spola i usmjerene su kod obje spine kraniomedijalno pod kutem od oko 45 stupnjeva.



Slika 19. Vektorski prikaz promjene oblika kraniofacijalnog skeleta kod ispitanika ženskog spola u razdoblju nakon menopauze (nakon 49.3 godina)

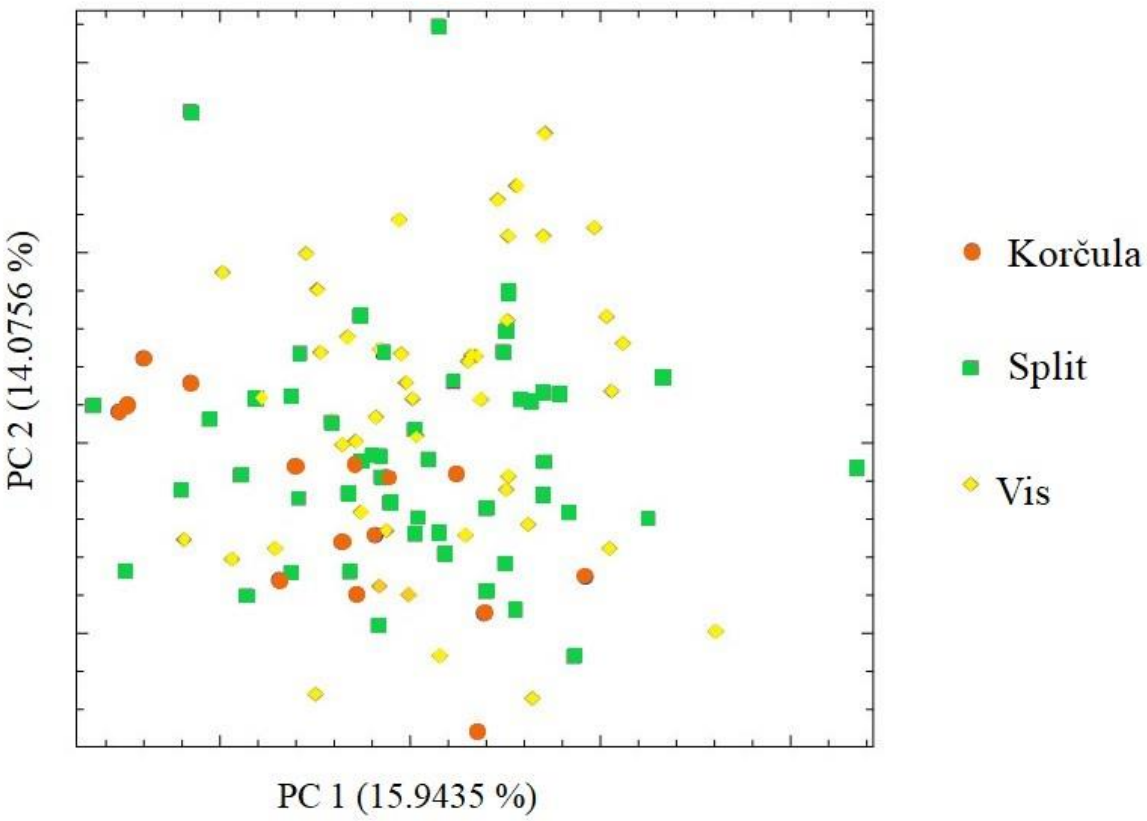
Slika 19. vektorski pokazuje promjene oblika kraniofacijalnog skeleta kod ispitanika ženskog spola u razdoblju nakon menopauze.

Promjene točke apertura piriformis desno (apr) i lijevo (apl), prosthion (pr), foramen incisivus (fi), anteriorna nazalna spina (ans), i infradentale (id) nisu vidljive.

Najizaženije promjene vidljive su na točkama zygoorbitale desno (zor) i lijevo (zol) (kaudolateralni smjer), zygomaxillare desno (zmr) i lijevo (zml) (kaudolateralni smjer), coronoid desno (cnr) i lijevo (cnl) (kraniolateralni smjer).

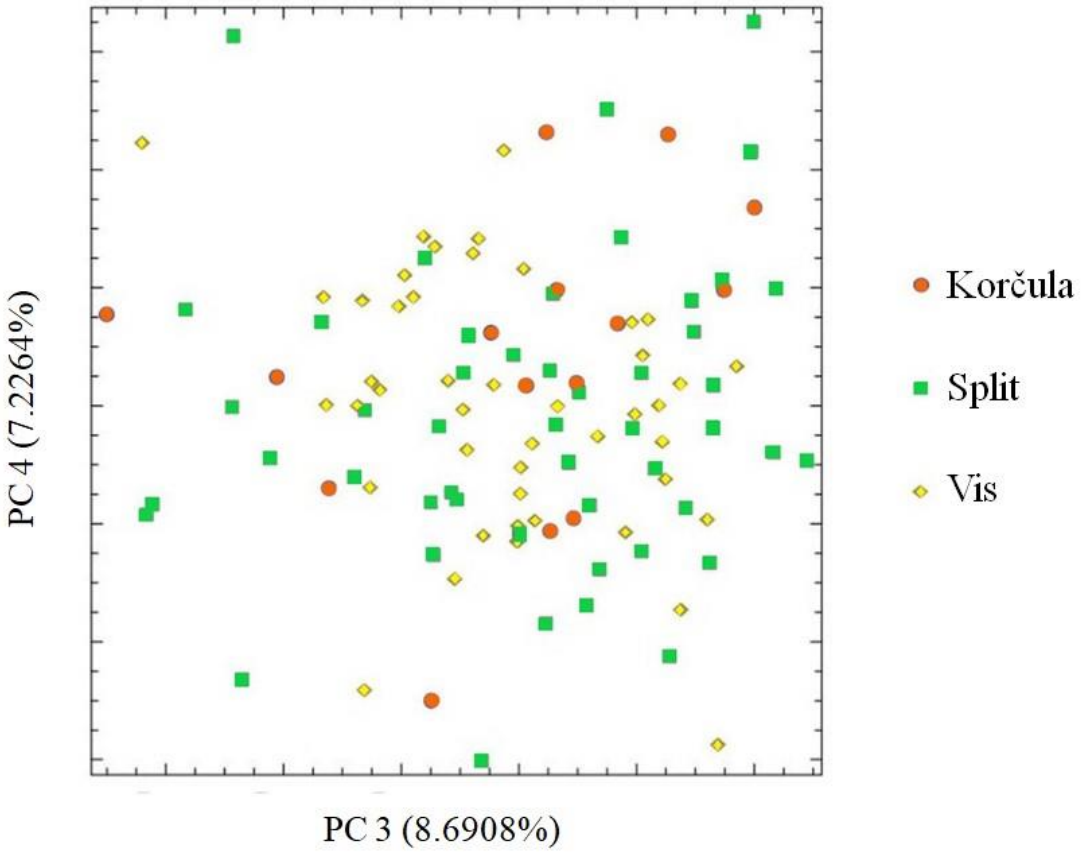
Promjene manjeg intenziteta vidljive su na točkama foramen mentale desno (fmer) i lijevo (fmel) (kranioanteriorni smjer) i foramen mandibule desno (fmar) i lijevo (fmal) (kraniposterioni smjer) te na točki spina nasalis posterior (pns) čiji je smjer promjena kaudalni i blago posteriorni.

4.2.4. Rezultati analize distribucije oblika kraniofacijalnog skeleta prema mjestu stanovanja



Slika 20. Prva i druga glavna komponenta distribucije oblika kraniofacijalnog skeleta na razini cijelog uzorka

Slika 20. prikazuje prvu i drugu glavnu komponentu distribucije oblika kraniofacijalnog skeleta na razini cijelog uzorka. Na ordinati su grafički prikazane vrijednosti prve glavne komponente, a na apsici vrijednosti druge glavne komponente za svakog ispitanika. Ispitanici označeni narančastim krugom pripadaju skupini Korčula, ispitanici označeni zelenim kvadratom pripadaju skupini Split, dok ispitanici označeni žutim rombom pripadaju skupini Vis. Vrijednosti glavnih komponenti označene na apscisi i ordinati predstavljaju odstupanje svakog pojedinačnog ispitanika od prosječnog uzorka. Kao što se može vidjeti na slici, ispitanici se prema mjestu stanovanja ne grupiraju u klastere.



Slika 21. Treća i četvrta komponenta distribucije oblika kraniofacijalnog skeleta na razini cijelog uzorka

Slika 21. prikazuje treću i četvrtu glavnu komponentu distribucije oblika kraniofacijalnog skeleta na razini cijelog uzorka. Na ordinati su grafički prikazane vrijednosti treće glavne komponente, a na apsici vrijednosti četvrte glavne komponente za svakog ispitanika. Ispitanici označeni narančastim krugom pripadaju skupini Korčula, ispitanici označeni zelenim kvadratom pripadaju skupini Split, dok ispitanici označeni žutim rombom pripadaju skupini Vis. Vrijednosti glavnih komponenti označene na apscisi i ordinati predstavljaju odstupanje svakog pojedinačnog ispitanika od prosječnog uzorka. Kao što se može vidjeti na slici, ispitanici se prema mjestu stanovanja ne grupiraju u klastere.

Iako se ispitanici prema mjestu stanovanja (Korčula, Split, Vis) ne grupiraju u klastere i među njima postoje mnoga preklapanja u obliku kraniofacijalog skeleta, F test je pokazao da među ispitanika Korčule i Visa postoji statistički značajna razlika u obliku kraniofacijalnog skeleta.

Tablica 8. Statistički značajna razlika u obliku kraniofacijalnog skeleta između ispitanika s različitih geografskih područja

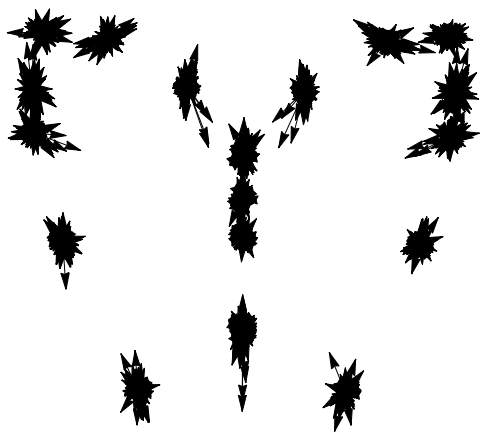
Skupine ispitanika	**p iznos**
Korčula/Split	0.062
Korčula/Vis	0.005
Split/Vis	0.315

Tablica 8. prikazuje rezultate statističke obrade oblika kraniofacijalnog skeleta kod ispitanika s područja Visa, Korčule i Splita izmjerenu F testom.

4.3. Rezultati analiza asimetrije kraniofacijalnog skeleta

4.3.1. Rezultati modeliranja preslike objekta i stvaranje simetričnog objekta

Integracijom svih promatranih točaka i usporedbom originalnog rasporeda točaka svakog ispitanika s vlastitom idealnom preslikom, za svakog je ispitanika utvrđeno vektorsko odstupanje točaka od tzv. referentnog oblika. Kao referentni oblik korištena je grafičko-matematička izračunana srednja vrijednost prostornog položaja svake od antropometrijskih točaka na razini cijelog uzorka.



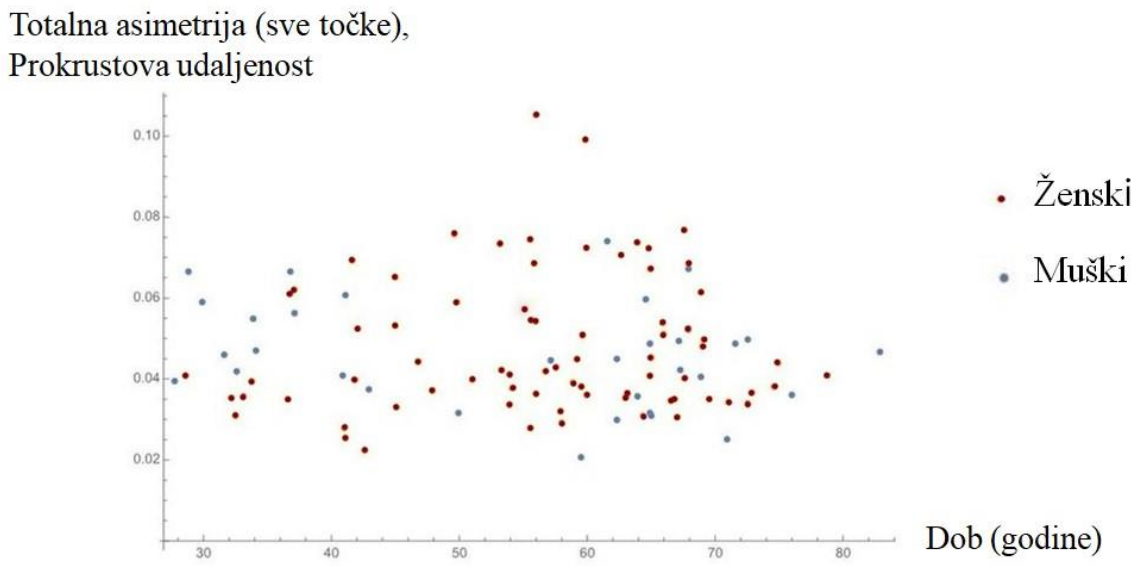
Slika 22. Vektorsko odstupanje točaka od referentnog oblika

Slika 22. prikazuje vektorsko odstupanje točaka od referentnog oblika nakon modeliranja preslike objekta i stvaranje simetričnog objekta. Slika prikazuje relativno ujednačeni intenzitet odstupanja, ali u različitim smjerovima. Na slici je posebno vidljivo odstupanje od referentnog oblika u orbitalnom i nazalnom dijelu kraniofacijalnog skeleta.

Statistička obrada ukupne, direkcije i fluktuacijske asimetrije provedena je metodom analize asimetrije prema Mardia i sur (2000.).

Metoda glavnih komponenata (*Principal Components Analysis*, PCA) ukazala je na distribuciju dominantnih varijacija oblika unutar različitih populacija i prikazala različitosti i sličnosti među njima.

4.3.2. Rezultati distribucije totalne asimetrije kraniofacijalnog skeleta na razini cijelog uzorka s obzirom na spol i dob

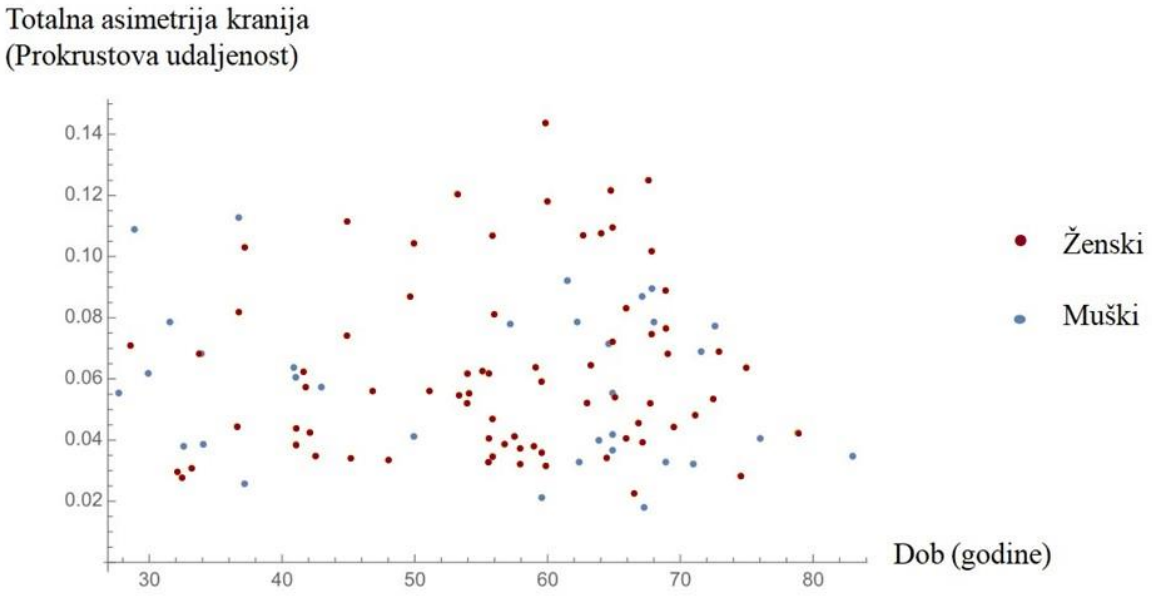


Slika 23. Distribucija totalne asimetrije kraniofacijalnog skeleta na razini cijelog uzorka s obzirom na spol i dob

Slika 23. prikazuje totalnu asimetriju kraniofacijalnog skeleta na razini cijelog uzorka s obzirom na spol i dob prikazanu kao Prokrustova udaljenost između svake individue i njegove simetrične refleksije.

Na x osi nalazi se dob ispitanika prikazana u godinama (u jedinicama od po 2 godine, počevši od 28 do završno 84 godine). Na y osi nalazi se iznos Prokrustove udaljenosti (u jedinicama od 0.005).

Plavi krugovi predstavljaju ispitanike muškog spola, a crveni krugovi ispitanike ženskog spola. Na grafu se vidi da se totalna asimetrija izražena u jedinicama Prokrustove udaljenosti ne grupira ovisno o dobi niti ovisno o spolu.

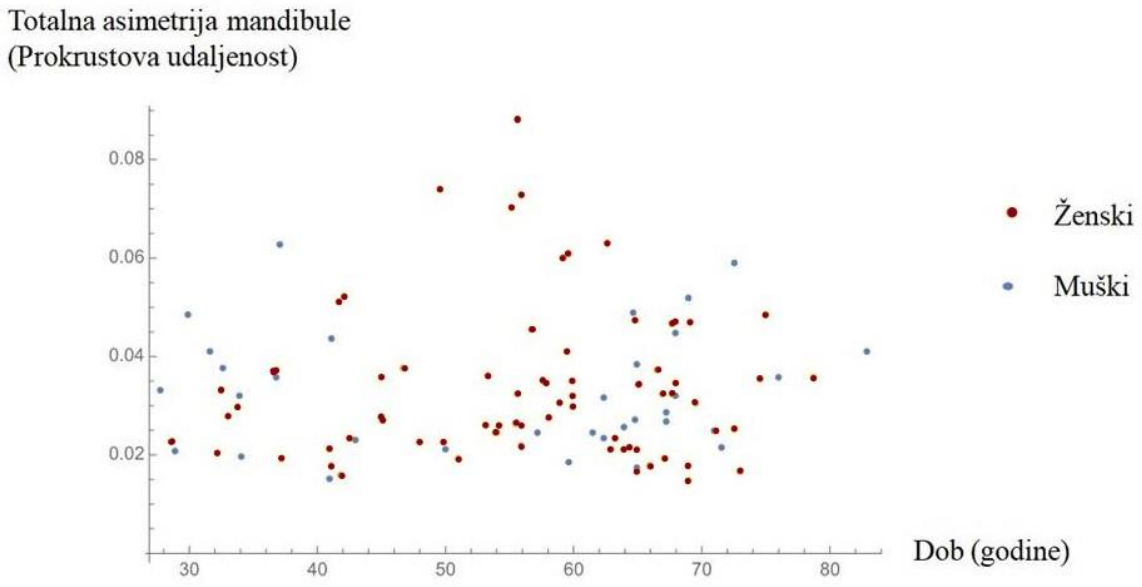


Slika 24. Distribucija totalne asimetrije za područje kranija na razini cijelog uzorka s obzirom na spol i dob

Slika 24. prikazuje totalnu asimetriju na razini cijelog uzorka s obzirom na spol i dob prikazanu kao Prokrustova udaljenost između svake individue i njegove simetrične refleksije za područje kranija. Na x osi nalazi se dob ispitanika prikazana u godinama (u jedinicama od po 2 godine, počevši od 28 do završno 84 godine). Na y osi nalazi se iznos Prokrustove udaljenosti (u jedinicama od 0.005).

Plavi krugovi predstavljaju ispitanike muškog spola, a crveni krugovi ispitanike ženskog spola.

Na grafu se vidi da se totalna asimetrija na područje kranija izražena u jedinicama Prokrustove udaljenosti ne grupira ovisno o dobi niti ovisno o spolu.

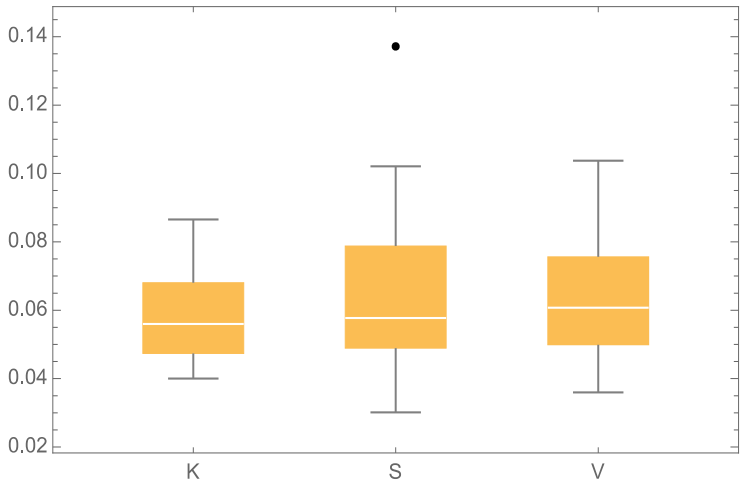


Slika 25. Distribucija totalne asimetrije za područje mandibule na razini cijelog uzorka s obzirom na spol i dob

Slika 25. prikazuje totalnu asimetriju na razini cijelog uzorka s obzirom na spol i dob pokazuje totalnu asimetriju prikazanu kao Prokrustova udaljenost između svake individue i njegove simetrične refleksije za područje mandibule. Na x osi nalazi se dob ispitanika prikazana u godinama (u jedinicama od po 2 godine, počevši od 28 do završno 84 godine). Na y osi nalazi se iznos Prokrustove udaljenosti (u jedinicama od 0.005).

Plavi krugovi predstavljaju ispitanike muškog spola, a crveni krugovi ispitanike ženskog spola. Na grafu se vidi da se totalna asimetrija na područje mandibule izražena u jedinicama Prokrustove udaljenosti ne grupira ovisno o dobi niti ovisno o spolu.

4.3.3. Rezultati analize totalne asimetrije prema mjestu stanovanja

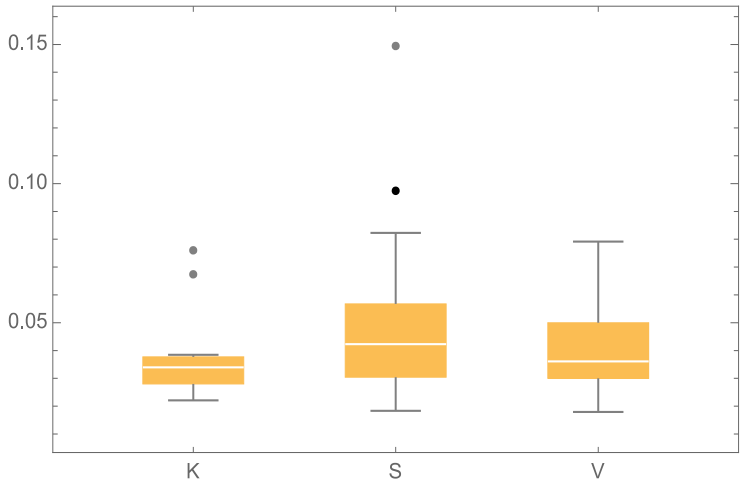


Slika 26. Prikaz iznosa totalne asimetrije za sve antropometrijske točke za područje cijelog kraniofacijalnog skeleta prema mjestu stanovanja ispitanika

Slika 26. pokazuje iznos totalne asimetrije za sve antropometrijske točke za područje cijelog kraniofacijalnog skeleta prema mjestu stanovanja ispitanika: ispitanici s područja Korčule (K), ispitanici s područja Splita (S), ispitanici s područja Visa (V).

Tablica 9. Iznosi srednjeg odstupanja, srednje vrijednosti i standardne devijacije za totalnu asimetriju za sve točke

	Korčula	**Split**	**Vis**
srednje odstupanje	0.0585	0.0631	0.0624
srednja vrijednost	0.0559	0.0577	0.0607
standardna devijacija	0.0142	0.0214	0.0162



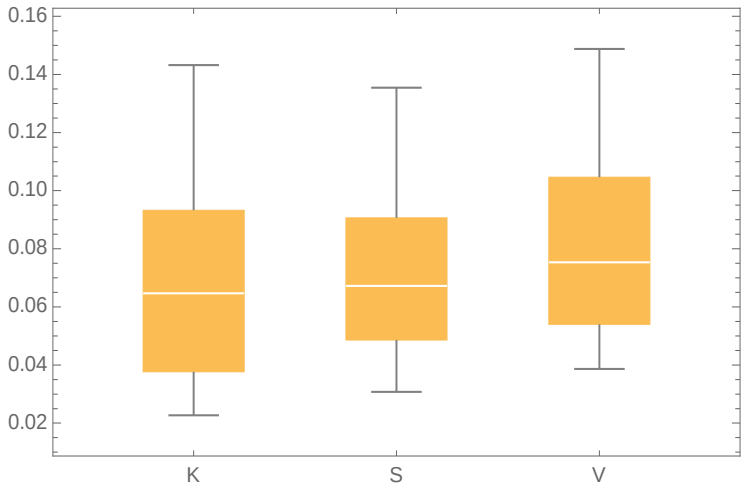
Slika 27. Prikaz iznosa totalne asimetrije za antropometrijske točke za područje kranija prema mjestu stanovanja ispitanika

Slika 27. pokazuje iznos totalne asimetrije za antropometrijske točke za područje kranija prema mjestu stanovanja ispitanika: ispitanici s područja Korčule (K), ispitanici s područja Splita (S), ispitanici s područja Visa (V).

Tablica 10. Iznosi srednjeg odstupanja, srednje vrijednosti i standardne devijacije za totalnu asimetriju za područje kranija

	Korčula	Split	Vis
srednje odstupanje	0.0368	0.0478	0.0395
srednja vrijednost	0.0339	0.0422	0.0360
standardna devijacija	0.0149	0.0231	0.0143

Tablica 10. pokazuje iznose srednjeg odstupanja, srednje vrijednosti i standardne devijacije za totalnu asimetriju za područje kranija, za područje Korčule, Splita i Visa.
Ispitanici s područja Splita imaju najviše srednje vrijednosti, ali i najviše srednje odstupanje.



Slika 27. Prikaz iznosa totalne asimetrije za antropometrijske točke za područje mandibule prema mjestu stanovanja ispitanika

Slika 27. pokazuje iznos totalne asimetrije za antropometrijske točke za područje mandibule prema mjestu stanovanja ispitanika: ispitanici s područja Korčule (K), ispitanici s područja Splita (S), ispitanici s područja Visa (V).

Tablica 11. Analiza varijance za totalnu asimetriju za sve točke

	stupnjevi slobode	**suma kvadrata**	**F vrijednost**	**P vrijednost**
dob	1	1.32716×10^{-6}	0.196119	0.658848
spol	1	4.40511×10^{-8}	0.0065096	0.935859
Vis	1	8.21234×10^{-6}	1.21357	0.273325
Korčula	1	4.31328×10^{-6}	0.63739	0.426588
inbreeding	1	7.83378×10^{-6}	1.15763	0.2846
ukupno	104	0.000703543		

Tablica 11. pokazuje analizu varijance (ANOVA) koja je pokazala da ne postoji statistički značajna razlika (R^2=0.094) u iznosu totalne asimetrije niti po dobi i spolu ispitanika, niti po mjestu stanovanja (Vis i Korčula), niti prema iznosu inbreedinga.

Tablica 12. Analiza varijance za totalnu asimetriju za područje mandibule

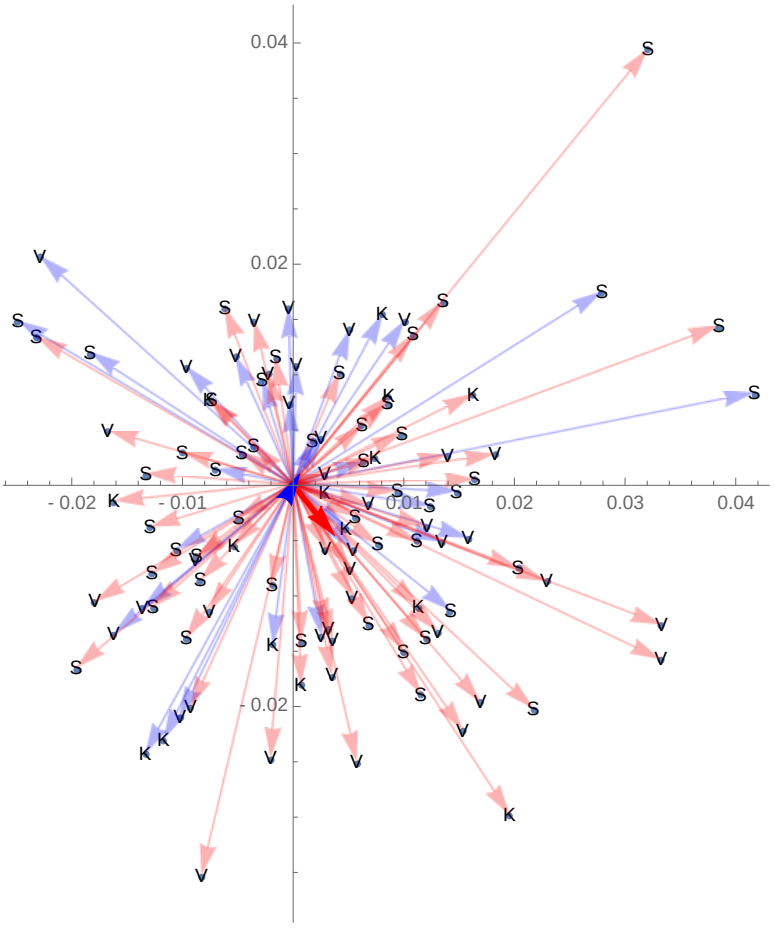
	stupnjevi slobode	suma kvadrata	F vrijednost	P vrijednost
dob	1	2.01489×10^{-8}	0.0000562266	0.994032
spol	1	0.0000203044	0.0566605	0.812336
Vis	1	0.000709825	1. 98081	0.162375
Korčula	1	0.00151117	4.21701	0.0426047
inbreeding	1	0.000694392	1.93774	0.166972
ukupno	104	0.0399487		

Tablica 12. pokazuje analizu varijance (ANOVA) koja je pokazala da ne postoji statistički značajna razlika (R^2=0.094) u iznosu totalne asimetrije za područje mandibule niti po dobi i spolu ispitanika, niti po iznosu inbreedinga. Ispitanici s područja Korčule statistički se razlikuju u iznosu totalne asimetrije za područje mandibule u odnosu na ispitanike Visa i Splita.

Tablica 13. Analiza varijance za totalnu asimetriju za područje kranija

	stupnjevi slobode	suma kvadrata	F vrijednost	P vrijednost
dob	1	2.01489×10^{-8}	0.186043	0.66715
spol	1	0.0000203044	0.0568841	0.811974
Vis	1	0.000709825	1. 25977	0.264357
Korčula	1	0.00151117	2.35992	0.127615
inbreeding	1	0.000694392	1.3871	0.241663
ukupno	104	0.0399487		

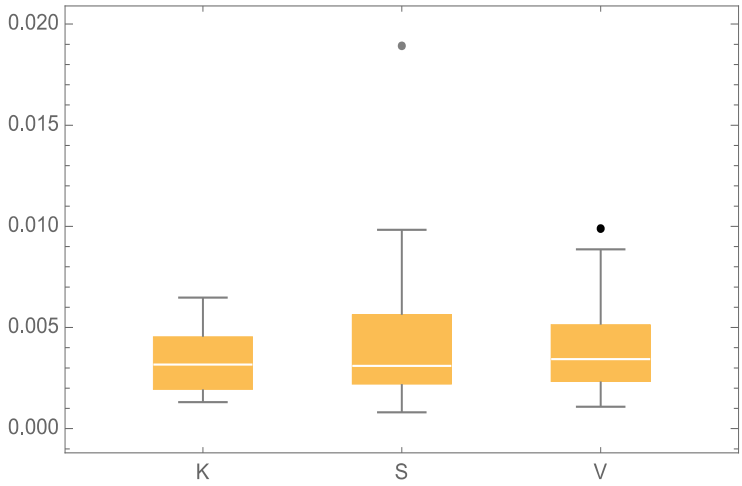
Tablica 13. Analiza varijance (ANOVA) pokazala je da ne postoji statistički značajna razlika (R^2=0.051) u iznosu totalne asimetrije za područje kranija niti po dobi i spolu ispitanika, niti po mjestu stanovanja (Vis i Korčula), niti prema iznosu inbreedinga.



Slika 28. Multivarijantni prikaz totalne asimetrije s obzirom na spol i mjesto stanovanja

Slika 28. pokazuje multivarijantni prikaz totalne asimetrije s obzirom na spol i mjesto stanovanja. Crveni vektori predstavljaju ispitanike ženskog spola, dok plavi predstavljaju ispitanike muškog spola. Oznake slovima predstavljaju populacije ispitanika ovisno o mjestu stanovanja: S - Split, K - Korčula, V - Vis. Graf ne pokazuje jasnu razliku u asimetriji između spolova (plavi i crveni vektori) ili između populacija (S, K, V).

4.3.4. Rezultati analize fluktuacijske asimetrije prema mjestu stanovanja



Slika 29. Prikaz iznosa fluktuacijske asimetrije za sve antropometrijske prema mjestu stanovanja ispitanika

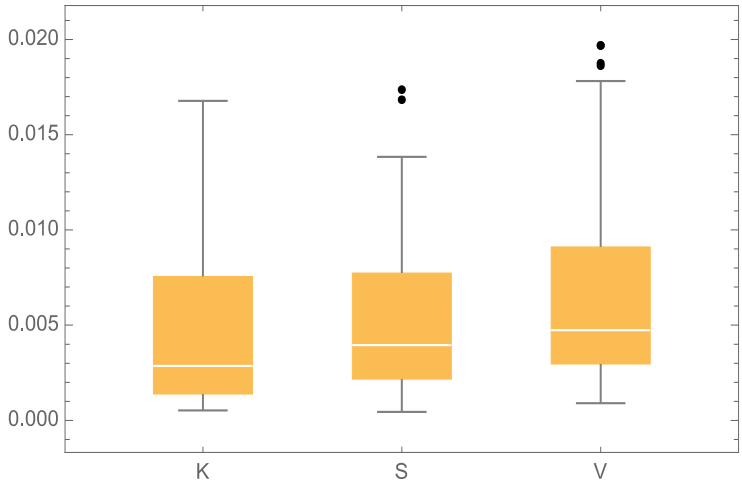
Slika 29. pokazuje iznos fluktuacijske asimetrije za sve antropometrijske točke prema mjestu stanovanja ispitanika: ispitanici s područja Korčule (K), ispitanici s područja Splita (S), ispitanici s područja Visa (V).

Tablica 14. Iznosi srednjeg odstupanja, srednje vrijednosti i standardne devijacije za fluktuacijsku asimetriju za sve točke

	Korčula	Split	Vis
srednje odstupanje	0.0034	0.0042	0.0039
srednja vrijednost	0.0031	0.0030	0.0034
standardna devijacija	0.0016	0.0031	0.0021

Tablica 14. pokazuje iznose srednjeg odstupanja, srednje vrijednosti i standardne devijacije za fluktuacijsku asimetriju za sve točke, za područje Korčule, Splita i Visa.

Srednje vrijednosti veoma su slične između skupina, dok je srednje odstupanje najviše za ispitanike s područja Splita.



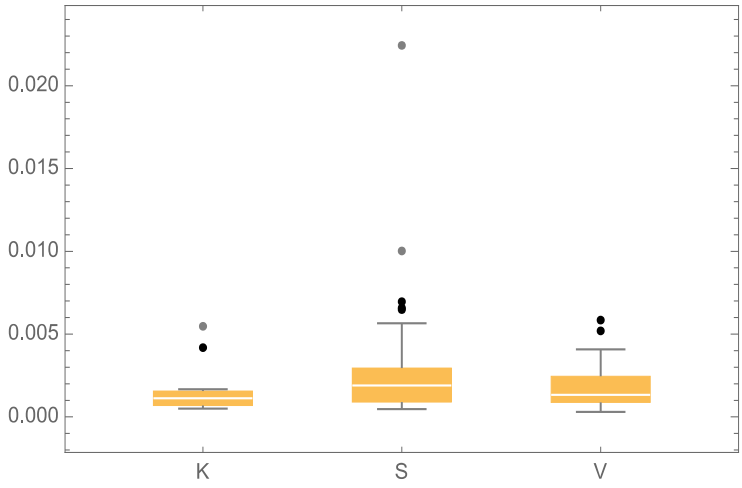
Slika 29. Prikaz iznosa fluktuacijske asimetrije antropometrijske točke kranija prema mjestu stanovanja ispitanika

Slika 29. pokazuje iznos fluktuacijske asimetrije za područje kranija prema mjestu stanovanja ispitanika: ispitanici s područja Korčule (K), ispitanici s područja Splita (S), ispitanici s područja Visa (V).

Tablica 15. Iznosi srednjeg odstupanja, srednje vrijednosti i standardne devijacije za fluktuacijsku asimetriju za područje kranija

	Korčula	Split	Vis
srednje odstupanje	0.0049	0.0054	0.0069
srednja vrijednost	0.0028	0.0039	0.0047
standardna devijacija	0.0048	0.0042	0.0053

Tablica 15. pokazuje iznose srednjeg odstupanja, srednje vrijednosti i standardne devijacije za fluktuacijsku asimetriju za područje kranija, za područje Korčule, Splita i Visa. Srednja vrijednost najviša je za ispitanike s područja Visa, kao i srednje odstupanje.



Slika 30. Prikaz iznosa fluktuacijske asimetrije za područje mandibule prema mjestu stanovanja ispitanika

Slika 30. pokazuje iznos fluktuacijske asimetrije za antropometrijske točke za područje mandibule prema mjestu stanovanja ispitanika: ispitanici s područja Korčule (K), ispitanici s područja Splita (S), ispitanici s područja Visa (V).

Tablica 16. Iznosi srednjeg odstupanja, srednje vrijednosti i standardne devijacije za fluktuacijsku asimetriju za područje mandibule

	Korčula	Split	Vis
srednje odstupanje	0.0015	0.0028	0.0017
srednja vrijednost	0.0011	0.0019	0.0013
standardna devijacija	0.0013	0.0034	0.0012

Tablica 16. pokazuje iznose srednjeg odstupanja, srednje vrijednosti i standardne devijacije za fluktuacijsku asimetriju za područje mandibule, za područje Korčule, Splita i Visa. Srednje vrijednosti veoma su slične između skupina, dok je srednje odstupanje najviše za ispitanike s područja Splita.

Tablica 17. Analiza varijance za fluktuacijsku asimetriju za sve točke

	stupnjevi slobode	suma kvadrata	F vrijednost	P vrijednost
dob	1	2.41949×10^{-7}	0.0355796	0.850765
spol	1	6.49487×10^{-7}	0.0955096	0.757923
Vis	1	8.34715×10^{-6}	1.22748	0.270529
Korčula	1	3.17378×10^{-6}	0.466717	0.496065
inbreeding	1	0.0000110059	2.1943	0.206228
ukupno	104	0.000725163		

Tablica 17. Analiza varijance (ANOVA) pokazala je da ne postoji statistički značajna razlika (R^2=0.053) u iznosu fluktuacijske asimetrije niti po dobi i spolu ispitanika, niti po mjestu stanovanja (Vis i Korčula), niti prema iznosu inbreedinga.

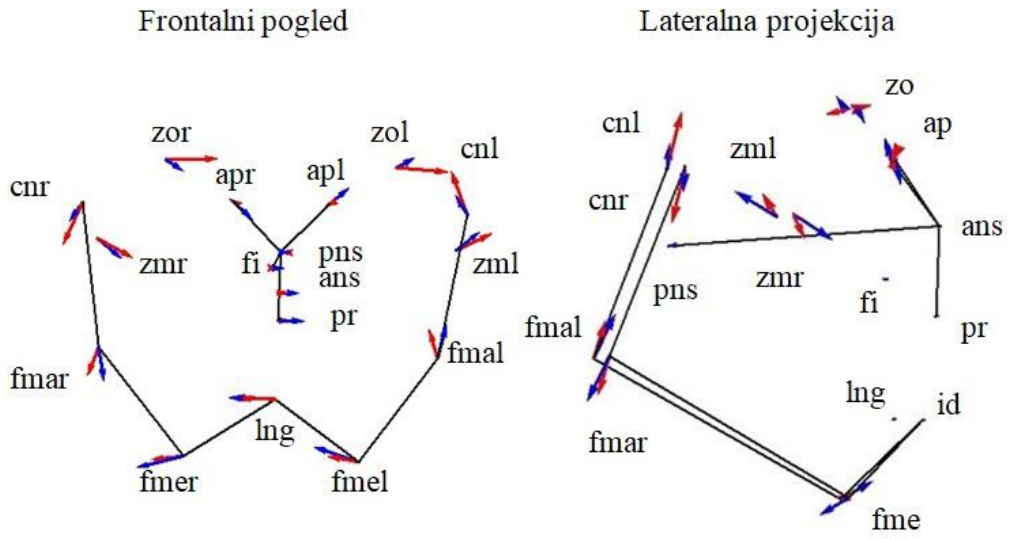
4.3.5. Rezultati analize direkcijske asimetrije prema mjestu stanovanja

Tablica 18. Iznosi direkcijske asimetrije

	sve točke	mandibula	kranij
Korčula	0.0121	0.00794	0.0192
Split	0.0123	0.00460	0.0188
Vis	0.0149	0.00590	0.0234

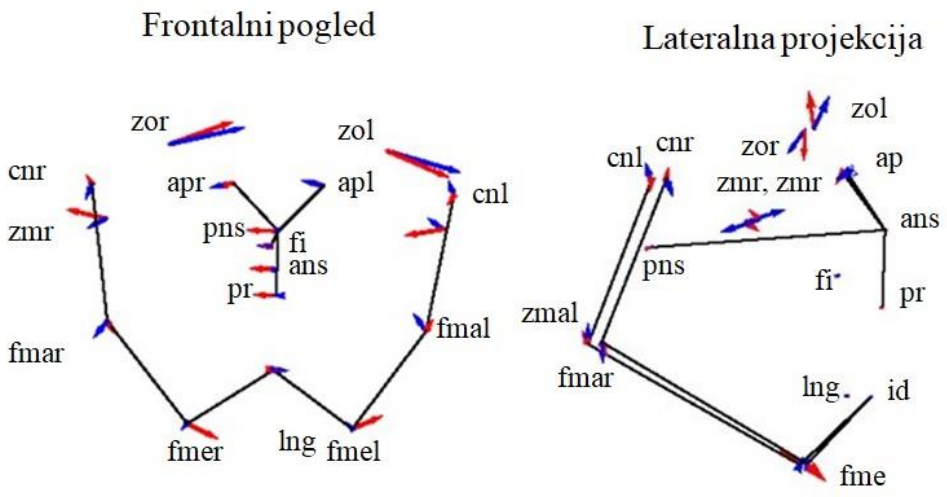
Tablica 18. pokazuje iznos direkcijske asimetrije u jedinicama Prokrustove udaljenosti (odstupanje od prosječnog asimetričnog obrasca). Iznos direkcijske asimetrije najmanji je za mandibulu za sve tri skupine ispitanika. Ispitanici s područja Visa imaju najveći iznos direkcijske asimetrije za cijelo područje kraniofacijalnog skeleta i za područje kranija, a ispitanici s područja Korčule najveći iznos direkcijske asimetrije mandibule.

4.3.6. Rezultati analize direkcijske i fluktuacijske asimetrije prema dobi



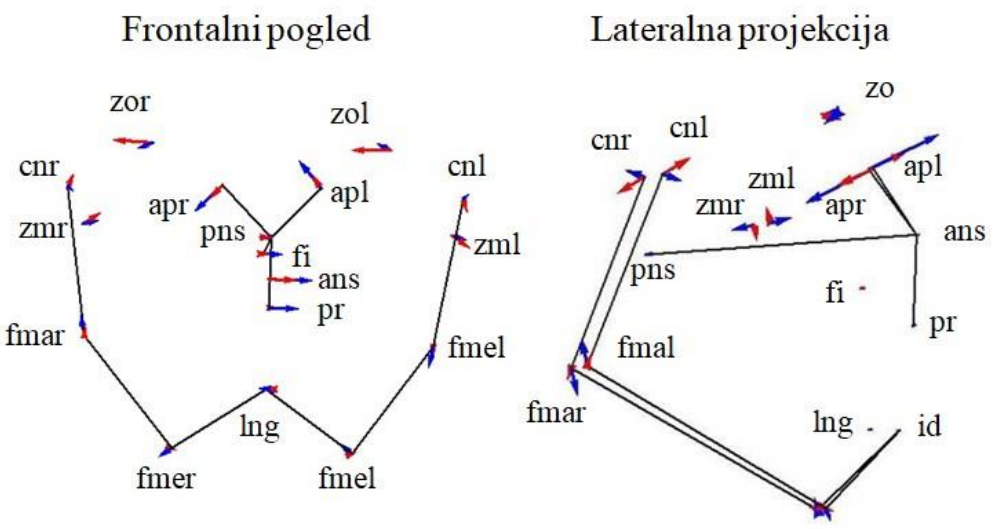
Slika 31. Prvi dominantni pravac fluktuacijske asimetrije (PC1 asimetričnih vektora)

Slika 31. pokazuje prvi dominantni smjer fluktuacijske asimetrije. Plavi vektori označavaju ispitanike mlađe od 55 godina, a crveni vektori ispitanike starije od 55 godina. Kako su crveni vektori duži od plavih, promjene smjera fluktuacijske asimetrije izraženije su kod ispitanika starijih od 55 godina. Najveće promjene vidljive su na zygoorbitalnom, nazalnom području i području coronida lijevog i desnog. Točke maksile (pr, ans, pns, fi) i mandibularna točka infadentale (id) gotovo se nisu pomaknule. Točke zygoorbitale i zygomaxillare pomiču se kod obje skupine prema lijevo u različitom iznosu stupnjeva, dok se točke mandibule (lng, fmer, fmel) pomiču prema desno. Te promjene prati pomak nosne aperture desno prema inferiorno, a lijeve prema superiorno. Iste se promjene vide i na točkama coronid i foramen mandibule: desni idu prema inferiono, a lijevi superiono.



Slika 32. Drugi dominantni pravac fluktuacijske asimetrije (PC2 asimetričnih vektora)

Slika 32. pokazuje drugi dominantni smjer fluktuacijske asimetrije. Plavi vektori označavaju ispitanike mlađe od 55 godina, a crveni vektori ispitanike starije od 55 godina. Promjene smjera flutuacijske asimetrije vidljive su kod svih ispitanika na cijelom kraniomandibularnom skeletu. Promjene koje se događaju i u prvom dominantnom pravcu vidljive su i ovdje, s razlikom što su najizraženije na točki zygoorbitale i da se kod ispitanika starijih od 55 godina pomiču i točke maksile (pr, ans, fi i pns) i to oštro prema desno pod 90 stupnjeva. Također veće promjene kod ispitanika starijih od 55 godina pokazuje i foramen mentale koji sada mijenja svoj smjer prema lijevo.



Slika 33. Analiza smjera direkcijske asimetrije

Slika 33. pokazuje smjer direkcijske asimetrije (kao odstupanje od simetrične sredine). Kako razlika u asimetriji između spolova i između populacija ovisno o mjestu stanovanja nije ukazana, ovdje plavi vektori označavaju ispitanike mlađe od 55 godina, a crveni vektori ispitanike starije od 55 godina. Promjene smjera direkcijske asimetrije vidljive su kod svih ispitanika na orbitalnom i nazalnom području, dok su promjene na području mandibule zamjetljivo male. Kako su crveni i plavi vektori nezamjetljivo različitih duljina, promjene smjera direkcijske asimetrije ne inteziviraju se s dobi. Točke zygoorbitale pomiču se prema desno što dovodi do promjene desnog coronoida posterokaudalno, a lijevog superokranijalno. Iste promjene, samo manjeg intenziteta, vidljive su na točki zygomaxilare lijevo i desno. Najveće promjene pokazuje točka apertura piriformis i to kod ispitanika mlađih od 55 godina. Kako se apertura rotira obrnuto od smjera kazaljke na satu, desna se pomiče laterokaudalno, a lijeva mediokranijalno.

5. DISKUSIJA

Sustavno se za života oblik lica mijenja rastući, sazrijevajući i stareći. Ono što vidimo na površini zajednički je učinak starenja i drugih procesa koji se događaju u nekoliko slojeva različitih tkiva, koštanih i mekanih. Unatoč varijacijama u načinu života i okolišu, prvi znakovi starenja lica postaju vidljivi u 20-im i 30-im godinama (164, 165).Starenje lica rezultat je kumulativnih dobnih promjena kože, mekog tkiva i kostura lica (166). Njegove manifestacije odražavaju kombinaciju djelovanja gravitacije, gubitka volumena lica, progresivne resorpcije kostiju, smanjenja elastičnosti tkiva i preraspodjele masti (167).

Kvantificiranje promjena oblika lica nije samo ključno u području rekonstrukcije lica i estetskog pomlađivanja, već je također važno u studijama prepoznavanja lica, interpersonalne percepcije i stereotipizacije. Brojne antropološke, morfološke, histološke, dermatološke i kirurške studije bavile su se starenjem lica. Pokazalo se da koštana tkiva duž orbitalnog ruba, posebno superomedijalno i inferolateralno, opadaju s porastom dobi, dok središnji orbitalni dijelovi ostaju relativno stabilni tijekom cijelog života (32). Povlačenje kosti u medijalnom dijelu lica i maksile u starijoj dobi pridonosi promjeni i produbljivanju nazolabijalnih nabora i povećanom „ravnanju“ lica (168, 33). Produžavanje nosa rezultat je povećanja piriformnog otvora dok se koštani rubovi povlače, osobito u procesu povlačenja maksile prema gore. Smanjeni tonus mekog tkiva također pridonosi opuštanju vrha nosa (33, 169). Nadalje, visina i duljina mandibule smanjuju se u starijoj dobi, dok se mandibularni kut povećava (34).

Nakon što je općom Prokrustovom analizom maknut faktor veličine kraniofacijalnog skeleta i preostale su samo varijacije oblika, izvršena je analiza istog na ispitanicima ovog istraživanja. Vektorska analiza oblika kraniofacijalnog skeleta kod ispitanika ženskog i muškog spola mlađih od 55 godina ukazala je na relativno ujednačeni intenzitet odstupanja, ali u različitim smjerovima. Na slici je posebno vidljivo odstupanje od referentnog oblika u orbitalnom i nazalnom dijelu kraniofacijalnog skeleta. Vektori crvene boje dulji su od plavih što označava da su promjene oblika kraniofacijalnog skeleta kod ispitanika ženskog spola većeg intenziteta od promjena kod ispitanika muškog spola. Za razliku od intenziteta, smjerovi crvenih i plavih vektora su slični što dovodi do zaključka da su i smjerovi oblika promjena kraniofacijalnog skeleta u odnosu na dob kod ispitanika muškog i ženskog spola slični.

Promjene točke zygoorbitale uzrokovane porastom dobi intenzivnije su kod ispitanika ženskog spola i usmjerene su kranijalno. Promjene točke apertura piriformis uzrokovane porastom dobi intenzivnije su kod ispitanika ženskog spola i usmjerene su kraniolateralno. Nema vidljivih promjena oblika s porastom dobi točke foramen incisivus kod ispitanika

muškog i ženskog spola. Promjene točke zygomaxillare uzrokovane porastom dobi iste su kod ispitanika muškog i ženskog spola i usmjerene su kod ispitanika muškog spola kraniolateralno, dok su kod ispitanika ženskog spola usmjerene kaudolateralno. Nema vidljivih promjena oblika s porastom dobi točke foramen mandibule i foramen mentale, dok se točka infadentale kod ispitanika ženskog spola pomiče prema kaudalno. U lateralnom pregledu vidi se da su promjene točke coronoid s porastom dobi događaju samo kod ispitanika ženskog spola i usmjerene su kaudomedijalno pod kutem od oko 60 stupnjeva. Promjene točke spina nasalis anterior i spina nasalis posterior uzrokovane porastom dobi također se događaju samo kod ispitanika ženskog spola i usmjerene su kod obje spine kraniomedijalno pod kutem od oko 45 stupnjeva. Promjene točke linguale uzrokovane porastom dobi intenzivnije su kod ispitanika ženskog spola i u oba spola usmjerene su kaudomedijalno.

Za razliku od navedenih promjena, vektorski prikaz promjena oblika kraniofacijalnog skeleta kod ispitanika ženskog spola u razdoblju nakon menopauze (nakon 49.3. godina) ukazuje da: promjene točke apertura piriformis, prosthion, foramen incisivus, spina nasalis anterior, linguale i infradentale nisu vidljive. Najizraženije promjene vidljive su na točkama zygoorbitale (kaudomezijalno), zygomaxillare (kaudolateralno), coronoid (kaudolateralno), foramen mentale (kaudolateralno) i foramen mandibule (kranijalno). Promjene manjeg intenziteta vidljive su na točki spina nasalis posterior čiji je smjer promjena kaudolateralni.

Mendelson i Wong primijetili su (166), kao što se može zaključiti i nakon vektorske analize oblika kraniofacijalnog skeleta ispitanika ovog istraživanja mlađih od 55 godina, da se projekcija lica smanjuje s dobi i da regija mandibule postaje relativno više konkavna (170, 171, 172). Vektorska analiza promjena oblika kraniofacijalnog skeleta s dobi djelomično je usuglašena sa studijom Karunanayake (173) koja se bavila analizom kraniofacijalnog remodeliranja. Ona je donijela zaključke kako je remodeliranje kostiju lica kod iste osobe, tijekom perioda od 10 godina, a praćeno analizom tvrdih tkiva na kompjuteriziranoj tomografiji, karakterizirano resorpcijom na: piriformnom otvoru; prednjem zidu gornje čeljusti, superocentralno, superomedijalno i inferolateralno oko orbitalnih obruba.

U literaturi, mnoge studije bave se dobnim kvantificiranjem obilježja oblika lica (174, 175), ali dokazi su još uvijek u velikoj mjeri kvalitativni. Kombiniranje te kvalitativne procjene oblika s oskudnim kvantitativnim studijama ometano je različitim etničkim podrijetlom promatranih populacija ispitanika (176). Zbog toga se ovo istraživanje oblika kraniofacijalnog skeleta promatralo pristupom geometrijske morfometrije na genetički i ekološki homogenoj

skupini ispitanika. Ovo istraživanje predstavlja potpuno kvantitativnu trodimenzionalnu analizu starenja lica. Ono pokazuje da se oblik lica mijenja u odrasloj dobi. Ovaj zaključak odnosi se i na kraniofacijalni skelet i na meko tkivo (42). Dok su se prethodne studije o starenju oslanjale na kvalitativne opise ili pojedinačna linearna ili kutna mjerenja (166), ova kvantitativna trodimenzionalna analiza starenja lica pokazuje da je obrazac starenja statistički značajno različit kod žena i kod muškaraca. U premenopauzalnom dijelu postoji zajednički prosječan obrazac starenja lica muškaraca i žena, ali prosječni tempo starenja dvaput je viši kod žene nego kod muškaraca. Ovaj zajednički obrazac starenja lica sadrži nekoliko lokalnih promjena oblika (npr. relativno manje oči, tanje usne) i prošireno donje lice (zbog opuštenijeg mekog tkivo) (42). Naši nalazi nalikuju 3D vizualizacijama starenja lica kineskih i čeških uzoraka (174, 175).

Po prvi put smo prikazali oštru i relativno iznenadnu razliku nakon menopauze od premenopauzalnog starenja lica, proučavajući i kraniofacijalni skelet u sklopu ovog istraživanja i meko tkivo na istoj skupini ispitanika (42). Razdoblje nastupanja menopauze vrijeme je kada se gubi zajednički linearni obrazac promjene skeleta i mekog tkiva lica s dobi na način da nakon menopauze krivulja promjene oblika lica žene postaje diskontinuirana s nepredvidljivim uzlaznim i silaznim varijacijama.

Prosječno vrijeme menopauze kod žena ovog uzorka je 49.3. godina, dok je meta-analizom utvrđeno kako je prosječno vrijeme nastupanja prirodne menopauze žena u Europi oko 50,5 godina (177).

Dijeleći uzorak ovog istraživanja u odnosu na prosječno vrijeme menopauze, vidimo da se s porašću dobi statistička značajnost u obliku kraniofacijalnog skeleta gubi i potpuno nestaje u grupi starijih od 55 godina.

Razlog navedenog najvjerovatnije je u činjenici da smanjenje različitih hormona uzrokuje statistički značajnu razliku u obliku kraniofacijalnog skeleta između žena i muškaraca. Kod žena dominira smanjenje estrogena, a kod muškarca smanjenje testosterona. Poznato je da oba hormona utječu na metabolizam kostiju, ali je resorpcija kosti primarno kontrolirana estrogenom kod oba spola (37, 38, 178). Gubitak estrogena također utječe na kosti čeljusti (39, 40).

Mnogo veće smanjenje estrogena u žena u odnosu na muškarce može uzrokovati izraženiju resorpciju kosti kod žena.

Nalazi ovog istraživanja također pridonose izvješću Shawa i suradnika (34) o povećanju mandibularnog kuta, smanjenju visine i duljine donje čeljusti kod oba spola, s najjačim učincima u ženskim postmenopauzalnim godinama. Ovi rezultati, zajedno sa značajnom povezanošću oblika lica s godinama od posljednje menstruacije žena u menopauzi, sugeriraju da varijacije u dobi u menopauzi doprinose individualnim varijacijama u izgledu i starenju lica. Slično tome, Chen et al naglasio je da su se Kinezi iste kronološke dobi razlikovali po plus ili minus šest godina u smislu „starosti lica“ (tj. starosti predviđene morfologijom lica) i da se iznos odstupanja povećava nakon 40. godine (174).

Oni su također razlog zbog čega su promjene s dobi veće kod žena nego kod muškaraca. U razdoblju menopauze i potpunog hormonskog disbalansa, mijenja se i prestaje djelovanje hormona koji dovodi do gubitka statističke značajnosti i nepredvidljivih promjena oblika kraniofacijalanog skeleta kod žena. Promjene hormonskog djelovanja vidljive su i kod muškaraca, ali su puno sporije i puno manjeg intenziteta.

Promatrajući vektorski prikaz promjene oblika kraniofacijalnog skeleta kod muškaraca i žena mlađih od 55 godina vidi se da su promjene koje se događaju starenjem izraženije kod žena, ali su smjerovi promjena isti kod oba spola. Kako je smjer svih anteriornih vektora orbitomaksilarne regije usmjeren prema superiono i posteriorno, a posteriornih vektora iste regije blago superiorno i anteriorno, možemo zaključiti da se srednji dio lica zaravnjava i smanjuje. Smjer vektora na mandibuli pokazuje da dolazi do fiziološke njezine blage posteriorne rotacije.

Nakon menopauze (49.3 godina) dolazi do znatnih promjena smjera vektora: mandibula anteriorno rotira uz istovremeni posterioni pomak struktura u srednjoj trećini lica što zajedno dovodi do smanjenja vertikalne dimenzije lica.

Značajan gubitak kostiju javlja se kod normalnog starenja i kod žena i kod muškaraca (179). Razvojna osteoporoza u starijoj dobi prirodna je posljedica gubitka koštane mase koja se događa s dobi. Višestruke poprečne i longitudinalne populacijske studije posljednjih 25 godina pomoću prostorne mineralne gustoće kostiju (aBMD) pomogli su definirati opći obrazac gubitka kosti koji se događa s normalnim starenjem. Oba spola gube aBMD počevši od oko 40 godina, a žene gube jedan BMD brže od muškaraca s početkom menopauze u kasnim 40-im ili ranim 50-im.

Nakon menopauze gubitak koštanog tkiva nastavlja se, ali sporije. Kod muškaraca je gubitak koštane mase s godinama manji i sporiji, počevši otprilike oko 40 godine (180).

Neovisno o promjenama u obrascu starenja, ovo istraživanje pokazalo je da je stopa starenja (prosječna veličina promjene oblika lica, bez obzira na uzorak promjene oblika) relativno konstantna kod muškaraca i da se povećava tek nakon 60 - 65 godina. Žene općenito imaju bržu prosječnu stopu starenja lica od muškaraca, ali je značajni početak rasta nastupio oko 52 - 55 godina; smanjio se s 57 na 60 godina i povećao nakon toga ponovno. Ovaj vremenski period dobro se slaže s nalazima hormonalnih promjena u longitudinalnoj studiji Randolph et al. Objavili su da se smanjenje koncentracije serumskog estradiola događa dvije godine prije zadnje menstruacije s maksimalnim smanjenjem neposredno oko zadnje menstruacije. Nakon toga, još dvije godine koncentracija se stabilizira na otprilike jednoj trećini razine prije smanjenja.

Brincat i kolege također su zaključili (181), na temelju širokog pregleda literature, da se 30 % kolagena kože izgubi u prvih pet godina nakon menopauze, s prosječnim padom od dva posto godišnje tijekom razdoblja od 15 godina. Slično tome, koristeći različite razine metilacije kao epigenetske markere starenja, Levine i kolege otkrili su da menopauza ubrzava biološko starenje (180).

Smanjenje i/ili usporavanje promjena sa starošću ima ogroman društveni i ekonomski interes za moderna društva. Estetska kirurgija prema podacima Američkog društva za estetsku plastičnu kirurgiju za 2017. (182) objavljuje da je u toj godini napravljeno 123 000 operacije kapaka kod žena i 22 300 kod muškaraca. Osim toga, kod oba spola bilo je 82 400 kirurških *faceliftova*, 22 700 podizanja obrva, 6 000 povećanja brade, 10 500 operacija uha, 54 700 presadbe masnog tkiva povezanog s licem, 28 500 podizanja vrata i 38 700 postupaka za estetsku operaciju nosa, a sve ne računajući nekirurške postupke. Većina ovih kategorija svake se godine povećava. Oko pedeset posto ukupnog broja operacija kapaka i *facelifta* proveden je u dobi od 51 do 64 godine, a oko trideset posto starijih od 65 godina.

Ovo naglašava važnost razumijevanja promjena koje ovise o dobi u morfologiji lica u starijoj dobi zajedno s njihovom socijalnom percepcijom.

Uzorci varijacije u prirodi odigrali su veliku ulogu u razvoju objašnjenja biološkog bogatstva na razini vrsta. Jedan takav utjecajni uzorak bio je morfološka posebnost malih populacija na otocima na periferiji velike kontinentalne kopnene mase (183).

Ako se otok razlikuje od kopna u staništu ili sastavu biološke zajednice, morfološke razlike često se mogu objasniti u smislu prilagodbe prirodnom selekcijom, odnosno adaptivnom diferecijancijom (184). Ali, ako su okoline manje-više iste, onda se mora tražiti objašnjenje na

drugom mjestu. Ako ispitanici Korčule i Visa dijele iste okolišne uvjete, onda objašnjenje za dobivenu statističku značajnost u obliku kraniofacijalnog skeleta moramo tražiti na drugom mjestu.

Prije pedeset godina, Ernst Mayr (185) sugerirao je da je ključ za evoluciju otoka u okolnostima i neposrednim posljedicama kolonizacije. Model koji je predložio, nazvan „model utemeljitelja učinaka“, pretpostavio je velike promjene u genetičkoj konstituciji novonastale populacije koje su pokrenute smanjenom genetskom varijacijom koju su proveli pojedini kolonizirajući pojedinci u osnivačkim povijesnim događajima.

Gubitak genetskih varijacija javlja se kada je nova populacija uspostavljena od strane vrlo malog broja pojedinaca iz veće populacije, a ti pojedinci nisu genetski reprezentativni za populaciju iz koje su došli (186, 187). Kao posljedica gubitka genetske varijacije, nova populacija može biti izrazito različita, i genotipski i fenotipski, od roditeljske populacije od koje je izvedena (188).

Efekt utemeljitelja bitan je za proučavanje otočne biogeografije i ekologije otoka. Prirodnu genetski „praznu ploču“ nije lako pronaći i istraživanja u tom smislu okrenuta su uglavnom na istraživanja otoka nakon velikih prirodnih katastrofa i povijesnih događanja. Povijesna događanja srednjodalmatinskog otočja i „privilegije Paštrovića“ definitivno su utjecala na razvoj reproduktivne izoliranosti ovog područja.

Populacije stanovništva Korčule i Visa primjer su reproduktivno i genetski izoliranih populacija kod kojih cijeli niz godina nije dolazilo do toka gena s okolnim populacijama, a posljedica čega je srođivanje. Kad u zatvorenoj populaciji imamo nositelje mutiranih gena, mutirano patološko svojstvo srođivanjem se može ispoljiti ili se njegova učestalost može povećati. Stoga su u zatvorenim populacijama mogući različiti nalazi, odnosno istraživano svojstvo može biti drugačije izraženo nego u općoj populaciji ili može potpuno nedostajati. Genetička posljedica srođivanja je povećanje udjela homozigota i recesivnih gena (189). Kad je recesivna mutacija odgovorna za neko svojstvo ili poremećaj, prevalencija svojstva ili poremećaja bit će veća u populaciji s većim koeficijentom srođivanja, nego što je to u općoj populaciji.

Heterozigotnost miješane, gradske populacije ne slijedi ovaj obrazac kao što bi se očekivalo jer je manje osjetljiva od alelne raznolikosti na učinke uzorkovanja (190). Ostaje otprilike ista među novim populacijama, bez obzira na njihovu dob, ali naglo opada kako se kreće od mladih do starih (185).

Razvojem prometne infrastrukture, teški uvjeti života i rada na otoku doveli su do sve veće migracije stanovništva i do sve veće povezanosti otoka i priobalnog splitskog područja. Sve ovo dovelo je do međusobnog miješanja stanovništva, dovelo je do miješanja homo i heterozigota već dugi niz godina.

Kako je to utjecalo na otočne populacije? Dva su bitna faktora koja su na to mogla utjecati: veličina otoka (populacije) i vrijeme utjecaja.

Model utemeljitelja u ono vrijeme bio je hrabro objašnjenje za genetička događanja jer se ništa nije znalo o genetskoj osnovi fenotipskih osobina. Poželjna metoda ispitivanja uključivala je laboratorijsko stvaranje novih populacija s nekoliko jedinki malih organizama s kratkim generacijskim vremenima (191, 192). Ova su eksperimentalna istraživanja dala neke odgovore (191, 193), ali uglavnom malo ili nimalo potpore (192, 194, 195) pitali su se jesu li genetske varijacije odraz znatnih promjena u vrijeme miješanja ili se jednostavno akumuliraju postupno tijekom vremena?

Nakon miješanja gradske i otočke populacije dolazi do uspostave nove populacije. Moguće je da se aleli u selektivno neutralnim lokusima izgube slučajnim genetskim pomakom i/ili dobiju mutacijom.

Može se očekivati da će genetičko zanošenje prevladati u manjim populacijama, barem neko vrijeme dok se ne postigne novo ravnotežno stanje mutacije, a populacije će se postupno divergirati. Ako se sve dogodi, zanošenje i mutacija, populacija se ne povećava velikom brzinom, a protok gena iz susjednih populacija je zanemariv ili nepostojeći, tada će veličina promjena unutar i između populacije biti funkcija vremena.

Varijacija u učestalosti gena između izvorne populacije i kolonije može također potaknuti dvije skupine da se značajno razlikuju tijekom mnogih generacija. Kako se varijacija, ili genetička udaljenost, povećava, dvije odvojene populacije mogu postati izrazito različite, i genetski i fenotipski. Njihovoj divergenciji doprinosi ne samo genetski zanos, već i prirodna selekcija, protok gena i mutacija. Može li se tako objasniti različitost kraniofacijalnog oblika ispitanika Korčule i Visa?

Nasuprot tome, ako se dogode događaji utemeljitelja, učinci mogu biti toliko jaki da preplavljuju učinke dugotrajnog genetskog zanošenja, ali se razlikuju među populacijama na način koji nije povezan s njihovim vremenom nastanka, već veličinom otočke populacije. Stoga se, u kontekstu dugotrajnog zanošenja, može istaknuti signal učinka utemeljitelja kao snažno smanjenje genetskih varijacija unutar populacija i velike razlike između susjednih populacija koje su se jednostavno akumulirale tijekom vremena (184). Može li se različitost u

obliku kraniofacijalnog skeleta ispitanika Korčule i Visa objasniti jačim utjecajem gradske, miješane populacije na ispitanike Visa s obzirom na to da i površinom i brojem stanovnika govorimo o manjoj populaciji u odnosu na Korčulu?

Kada je novoformirana kolonija mala, njezini osnivači mogu snažno utjecati na genetski sastav stanovništva daleko u budućnost. Moguće da se upravo to dogodilo sa skupinom ispitanika s područja Visa. Kod ljudi koji imaju nisku stopu reprodukcije, populacija će ostati mala za mnoge generacije, učinkovito pojačavajući stvaranje učinka genetičkog zanosa generacijama nakon, dok populacija ne dosegne određenu veličinu.

Aleli koji su bili prisutni, ali relativno rijetki u izvornoj populaciji, mogu se pomaknuti u jednu od dvije krajnosti. Najčešća je da je alel uskoro potpuno izgubljen, ali druga mogućnost je da alel preživi i za nekoliko generacija postaje mnogo raspršeniji u cijeloj populaciji.

Trodimenzionalna (3D) snimka kraniofacijalnog skeleta idealan je neionizirajući, neinvazivnan i veoma precizan materijal za fenotipske i fenomenske studije. Analiza tog vrijednog materijala prirodna je dopuna genetskim i epigenetskim tehnologijama koje imaju cilj olakšati napredak i razumijevanje pojedinih fenotipskih obilježja lica, kao što je npr. asimetrija (196),

Lice je jedinstvena refleksija primordijalnog tkiva, a postoje i dokazi koji podupiru primjenu 3D analize lica za istraživanje varijacija i bolesti, uključujući studije koje pokazuju da lice može odražavati sustavno zdravlje, pružati dijagnostičke tragove za poremećaje i da fenotipske varijacije lica odražavaju puteve fiziološke prilagodbe na vanjske okolišne čimbenike. Osim toga, varijacija lica povezuje se i s evolucijskim čimbenicima (103).

Fenotipske studije su dodatak (epi) genetskim i funkcija im je olakšati napredak u razumijevanju genomskih varijacija, genomskih utjecaja na fenotipove, istraživanja pleiotropije i otkrivanje složenih fenomena uključujući zdravlje i evolucijsku sposobnost (197). Tehnike nastajanja trodimenzionalne snimke lica i analiza tih snimaka geometrijskom morfometrijom pružaju objektivni materijal za identificiranje suptilnih varijacija lica i osnova su za nove pristupe u ispitivanju stanične biologije (198). Ti se pristupi odnose na „normalne“ fenotipske varijacije lica u što spada i asimetrija (199).

Asimetrija je opisana u velikom broju genetskih sindroma. Povezuje se s mutacijom CHD7 gena kod Charge sindroma. Uz mutaciju događa se i remodelacija kromatina (200) što je temeljni epigenetički proces (201). Ostali poremećaji povezani s asimetrijom lica uključuju gene kao što su geni RAS-MAPK mreže koje su u razvojnim putovima važnim za određivanje, rast i diferencijaciju staničnih linija. Nadalje, komponente RAS-MAPK puta mogu utjecati i na imunološki posredovane fenotipove (202). Stoga, procjena asimetrije lica može pružiti nove podatke za istraživanje kompleksnih fenotipova, a koje se povezuju s varijabilnim imunološkim odgovorom na cjepivo.

Direkcijska ili međugrupna asimetrija definira se kao genetska tendencija da se određeno svojstvo dosljedno razvija na različite načine na lijevoj i desnoj strani lica. Ona se može kvantificirati kao razlika između lijevog i desnog prosjeka i smatra se genetskim determiniranom. Njezin najupadljiviji primjer je asimetrija unutarnjih organa svih sisavaca i nekih vrsta biljaka, a najjači utjecaj vidi se u ranom stadiju razvoja. Pronađeni su i različiti molekularni mehanizni koji mogu biti razlog početne razlike između lijeve i desne strane (203, 204, 205, 206). To se naročito vidi kod kralježaka kod kojih je pokazano da je

ekspresija određenih gena u određenom dijelu ranog procesa organogeneze prisutna samo na jednoj strani organizma (207, 208). Većina ovih asimetrično ekspresiranih gena su signalni faktori i regulatorni geni koji ne kontroliraju samo morfogenetske asimetrične događaje organogeneze, već imaju važnu ulogu u razvoju u površinskom pojavljivanju asimetričnog fenotipa.

Okolišno funkcionalno i adaptivno razvojno usmjeravanje direkcijske asimetrije je, unatoč genetskim saznanjima, i dalje nejasno i na eksperimentalnoj razini (49, 209, 210), ali jasno je da se asimetrija mnogih vanjskih anatomskih struktura novorođenčeta smatra posljedicom neadaptibilnosti i razvojnih ograničenja. Na sreću, takva razvojna ograničenja rijetka su i vidljiva u sklopu kliničke slike genetskih sindroma, a direkcijska asimetrija najčešće se vidi kao mala klinička promjena nastala samo kao posljedica što morfološke strukture lijeve i desne strane ne rastu replicirajućim, istim procesima, već je puno površinskih razlika u ekspresiji površinskih signala lijeve i desne strane tijela.

Direkcijska asimetrija rasprostranjena je i predstavlja uobičajeni genomski utjecaj koji istovremeno djeluje i na lijevu i na desnu stranu te se ne smatra mjerilom razvojne nestabilnosti. Ipak, njezin utjecaj na konačni izgled fenotipa ne smije se zanemariti.

Za razliku od fluktuacijske asimetrije koja odražava stohastička odstupanja od savršene simetrije zbog okolišnih čimbenika i/ili epigenetskog stresa, direkcijska asimetrija i antisimetrija su genetske prirode (66, 109, 211, 212).

Razmišljajući u tom pravcu, rezultati ovog istraživanja pokazali su da je iznos direkcijske asimetrije najmanji i to nekoliko puta za područje mandibule za sve ispitanike što nas navodi na zaključak kako je utjecaj genotipa kod ovih ispitanika na područje mandibule najmanji i da sav uzrok nastanka fluktuacijske asimetrije mandibule ove populacije treba promatrati kao utjecaj okoliša. Kako je iznos fluktuacijske asimetrije mandibule najveći za područje Splita, nameće se i da je jak okolišni gradski utjecaj grada Splita. Iznosi i totalne i fluktuacijske asimetrije mandibule manji su od kranija što općenito govori da okoliš manje utječe na asimetriju mandibule i da je utjecaj na kranij puno jači. Totalna asimetrija mandibule je statistički značajno manja kod ispitanika s područja Korčule, a istovremeno je direkcijska kod ove populacije najveća što znači da je sam iznos totalne zapravo direkcijska i da asimetrija mandibule ispitanika s područja Korčule gotovo nije uopće pod okolišnim utjecajem i da je utjecaj okoliša na nasatanak asimetrije mandibule ispitanika s područja Visa i Splita mnogo

veći. Slične razlike u iznosu direkcijske asimetrije mandibule miševa u odnosu na ostali skelet dobili su i Leamy, 1998 (213) i Klingenberg, 2003 (214).

Kako su najveći iznosi DA na cijelo kraniofacijalno područje, područje kranija i mandibule podijeljeni između otočkih populacija, možemo razmišljati u smjeru jačeg genetskog utjecaja na fenotip obiju populacija uspoređujući ih s populacijom grada Splita. Kako je FA mandibule najveća za područje Splita, najveći je i utjecaj okoliša i to je u potpunoj suprotnosti s utjecajem na asimetriju mandibule ispitanika s područja Korčule. FA za cijeli kraniofacijalni skelet i za kranij najveća je ispitanike s područja Visa što također pokazuje jak utjecaj okoline. Taj utjecaj okoline koji je očito jači na području Visa i Splita u odnosu na više izoliranu populaciju Korčule međusobno se nadmeće i dovodi do toga da je totalna asimetrija kranija i mandibule najveća kod ispitanika s područja Visa, ali je za cijelo kraniofacijalno područje najveća kod ispitanika s područja Splita. Sve ovo nas navodi na zaključke: okolišni utjecaj je jak u nastanku asimetrije i on je populacije Splita i Visa unatoč genetskim razlikama učinio sličnima. Mikroklima, specifičnosti okolišnih faktora, odnosno njihov slab utjecaj i izoliranost na području Korčule učinili su da se specifičnost genotipa ispolji kao najmanja TA mandibule. Sve ove rezultate ispravno je sagledavati i kroz prizmu dobi budući da se radi o starijoj populaciji kada se utjecaj genetike, iako još djelotvoran, smanjuje i sve je veći utjecaj okolišnih faktora. Kako je utjecaj okolišnih faktora očigledno mali na Korčuli, sva asimetrija mandibule, iako statistički značajno mala, treba se gledati pod svjetlom isključivo genetskog utjecaja.

Novija istraživanja direkcijske asimetrije na kraniofacijalnom skeletu pokazuju različite rezultate. Studija o ljudskim lubanjama (215) nije pronašla direkcijsku asimetriju oblika, dok je nekoliko drugih izvijestilo o direkcijskom smjeru asimetrije lubanje (216, 217, 218, 219, 220, 221) i mekih tkiva lica i ušiju (70, 222, 223, 224, 225, 226.)

Ovo istraživanje pokazalo je postojanje direkcijske asimetrije cijelog kraniofacijalnog skeleta kod svih triju skupina ispitanika. Ispitanici s područja Visa imaju najveći iznos direkcijske asimetrije za cijelo područje kraniofacijalnog skeleta i za područje kranija, a ispitanici s područja Korčule najveći iznos direkcijske asimetrije mandibule. Kako ispitanici s područja Visa imaju i najveće iznose fluktuacijske asimetrije, genetički i okolišni utjecaji na kraniofacijalni skelet očito su nešto veći u skupini s područja Visa.

Promatrajući smjer direkcijske asimetrije kod ispitanika ovog istraživanja, vidljive su kod svih triju skupina (Korčula, Split, Vis) veće promjene na orbitalnom i nazalnom području, dok

su promjene na području mandibule zamjetljivo male što je i očekivano u odnosu na numeričke podatke. Nadalje, uspoređujući razliku iznosa direkcijske asimetrije starenjem vidimo da nema značajno različitih promjena direkcijske asimetrije s dobi što je u skladu s činjenicom da se najveće promjene direkcijske asimetrije vide u ranom stadiju razvoja i to pod utjecajem genotipa. Promjene smjera pojedinih točaka kao posljedica direkcijske asimetrije mogu se intepretirati kao odgovori genotipa na dobne promjene kraniofacijalnog skeleta. Najveće promjene pokazuje točka apertura piriformis i to tako da se se apertura rotira obrnuto od smjera kazaljke na satu, desna se pomiče laterokaudalno, a lijeva mediokranijalno. Te promjene dovode do iskrivljenja nosnog dijela prema desno.

Asimetrija lica uključena je i u evolucijske procese za koje se pretpostavlja da utječu na patogenezu složenih bolesti (227). Asimetrije lica uključene su i u preferencije u odabira partnera (228) za koje se zna da su evolucijski uvjetovane. U tom kontekstu, simetrija lica kod žena, koja je u korelaciji s varijacijom lokusa bez MHC-a, utvrđena je kao atraktivna osobina koju su ocijenili muškarci (228). Također, u subjektivnom smislu usporedbe monozigotnih parova blizanaca, lica blizanki s percipiranom simetrijom ocijenjena su kao atraktivnija i ta uočena privlačnost bila je izravno povezana sa smanjenom veličinom asimetrije (229). Studije također sugeriraju interaktivni učinak između varijacije MHC-a (228) i atraktivnosti lica na izbor partnera (a varijacija MHC povezana je s mnogim imunološki posredovanim bolestima i uz otpornost na infekcije (230). Prema Farkas, 2005. (90), fenotipski izgled lica povezuje se s: okolišnim uvjetima, socioekonomskim statusom i navikama prehrane.

Razvojna stabilnost odražava sposobnost genotipa da se razvija na isti način pod različitim uvjetima okoline. Odstupanja od razvojne stabilnosti, koja proizlaze iz disruptivnih učinaka okolišnih i genetskih stresova (231) mogu se mjeriti u smislu fluktuirajuće asimetrije što je posebno osjetljiv pokazatelj sposobnosti suočavanja s tim stresovima tijekom ontogeneze (232).

Socioekonomski status klasa majke, klasa oca, osobine sanitarnog čvora, statusni položaj u društvu kao odrasli, sve to pojačava vrijednost simetrije lica kao osjetljivi marker razvojne perturbacije i sugerira moguće mehanizme kojima se socioekonomski status povezuje sa zdravljem i sposobnošću prilagodbe (233). Takvi mehanizmi mogu uključivati razinu prehrane u djetinjstvu, kvalitetu liječenja bolesti ili roditeljskog ponašanja u odnosu na pušenje i/ili konzumaciju alkohola. Kao što je predviđeno statističkim vezama ranog razvoja sa zdravljem (234) i hipoteze unutar okvira razvojnih izvora (235), posljedice uskraćivanja djetinjstva trajale su: one su ostale uočljive u izmjerenoj simetriji lica više od 70 godina kasnije. Specifičnost ovog povezivanja na socioekonmski status ranog životnog vijeka, a ne na trenutni status životne sredine, a unatoč tome što je bliži vremenskom rasporedu i dalje podržava hipotezu da je djetinjstvo osjetljivo razvojno razdoblje.

Dok sadašnji rezultati ukazuju na to da signali simetrije lica signaliziraju okolišni čimbenici i to nije sporno, genomski utjecaj genetskih i/ili epigenetski čimbenici u simetriji lica i dalje je podložan istraživanjima. Nedavni dokazi upućuju da jedsposobnost generiranja alternativnih fenotipova na temelju epigenetske modifikacije može pomoći organizmu svladati stres i smanjiti trenutnu osjetljivost bolesti, ali sve to na trošak niže kondicije kasnije u životu (236,

237). Uzimajući ove nalaze u obzir, moguće je da simetrija lica odražava interakciju stresa s genetskom odgovornošću.

Istraživanje fluktuacijske asimetrije zubnog luka, kao i na orofacijalnom skeletu na arheološkim ostacima prehistorijske populacije Amerikanaca pronađene u dolini rijeke Ohio, pokazale su znatno veću asimetriju ove populacije u odnosu na kasnije prehistorijske populacije i u odnosu na populacije današnjeg doba. Veća razina razvojnog stresa tog ranijeg doba koja je dovela do veće asimetrije povezuje se s nepoznavanjem utjecaja konsangviniteta, ali i s načinom prehrane i općenito težim načinom života (238).

Rezultati ovog istraživanja pokazali su kako se totalna asimetrija izražena u jedinicama Prokrustove udaljenosti ne grupira ovisno o dobi niti ovisno o spolu. To je u suprotnosti s istraživanjima (198, 222) koji su pokazali da se asimetrija ljudskog lica razlikuje među spolovima, njezina veličina ovisna je o dobi i najveća je ranije u životu. Ti nalazi slažu se i s Rotterdamskim istraživanjem (239) u kojem su totalna i fluktirajuća asimetrija značajno povezane s dobi i spolom. Razlozi za te oprečne nalaze, a uzevši u obzir da se asimetrija s dobi smanjuje, možda leže u različitoj dobnoj strukturi ispitivanih populacija, odnosno starijoj dobnoj strukturi otočke populacije koja je bila predmet ovog istraživanja. Suprotno tome, Otremski i sur. i Penke i sur. Otkrili su da je povišena fluktuacija asimetrija prisutna kod starijih osoba (240, 241) (za razliku od relativno dosljednog smanjenja fluktuacijske asimetrije od rođenja do zrele odrasle dobi (240). Intuitivno razumna, ali bez čvrstih empirijskih dokaza, je sugestija da različite strane lica mogu različito stariti (167), primjerice zbog asimetričnog izlaganja suncu (242) - krajnji primjer lica vozača kamiona.

Učinak starenja na asimetriju također se razlikuje između crta lica: bočna asimetrija nosa s godinama postaje oštrija i stabilnija od brade (243). Ovo istraživanje pokazuje da se promjene fluktuacijske asimetrije s dobi povećavaju, odnosno da je okolišni utjecaj sve veći. Utjecaj je sve veći kako se udaljavamo od točaka u medijalnoj liniji pa se točke prostion, anteriorna nazalna spina, posteriorna nazalna spina, foramen incisivus i infradentale gotovo uopće ne pomiču, a najlateralnije točke ramusa, zygoorbitale i zygomaxillare pomiču se najviše i dovode do pomicanja kranijalnog dijela na lijevo, a mandibulranog na desno. Posljedično tome pomiče se i nosni dio i to tako da desna nosna apertura ide inferiorno, a lijeva superiorno.

Na utjecaj seksualnog dimorfizma na facijalnu asimetriju zbog različitog djelovanja X i Y kromosoma ukazao je i Alvesalo, 1997 (244). Ta različitost u hormonskom odgovoru i

balansu naročito je izražena u vrijeme rasta koštanih struktura i u vrijeme promjene hormonalnog statusa žena u vrijeme menopauze.

S obzirom na sve gore navedeno, možemo zaključiti kako genetski utemeljena direkcijska asimetrija lica može varirati ovisno o dobi i spolu, a evolucijske promjene nastale kao odgovor na vanjske utjecaje u podlozi su fluktuacijske asimetrije. Genetska podloga pojedinca svakako je predisponirajući čimbenik za manje ili više uspješnu prilagodbu. Evolucijski i tijekom života ljudsko se lice kontinuirano mijenja i prilagođava. Njegov rast i razvoj ima snažan evolucijski pečat kojim se zorno potvrđuju evolucijski mehanizmi prilagodbe i promjene morfologije nastale međudjelovanjem gena, okoliša i njihove interakcije. Fluktuacijska asimetrija kao evolucijski mehanizam prilagodbe smatra se mjerom razvojne nestabilnosti, odnosno neadekvatne prilagodbe na zahtjeve okoliša. Ona je zamjena za nepreciznost ljudskog razvoja koja je rezultat srođivanja i genetske homozigotnosti (245).

Istraživana populacija otoka Korčule i Visa rijedak je i vrijedan primjer izolirane populacije. Unatoč ukupnoj niskoj razini diferencijacije u humanoj populaciji, lokalni faktori kao što su geografska i kulturalna izolacija uvelike mogu utjecati na genetički diskontinuitet. Jasno razlikovani genetički izolati vrlo su vrijedni za mapiranje rijetkih genetskih bolesti i razjašnjavanje mehanizma nastanka složenih genetičkih oboljenja (141). Danas su primjeri izoliranih populacija veoma rijetki, jedna od njih je stanovništvo Sardinije u regiji Ogliastra, u Daghestanskim visoravnima i planinskim područjima Bosne (246). Zajednice istočnih jadranskih otoka Dalmacije bili su i još su uvijek predmet opsežnih antropoloških studija. S obzirom na udaljenost, pokazuju visok stupanj izolacije, endogamije i križanja. Prethodne genetičke studije koristeći serološke markere, maleni broj STR markera i analizirajući mitohondrijsko nasljeđivanje i markere Y kromosoma ukazale su na smanjenu raznolikost u otočkim populacijama u usporedbi s općom hrvatskom populacijom i visok stupanj diferencijacije među i unutar otočke populacije, a sve u skladu s djelovanjem jakog genetičkog utjecaja (134). Analiza mitohondrijske DNA (135) i markera Y kromosoma (136) pokazuje da je skupina višestrukog, raznorodnog podrijetla. To i ne iznenađuje budući da su jadranski otoci svjedok burne povijesti koja se događala na glavnim raskrižjima između Europe i Bliskog istoka. Demografska povijest svake otočne zajednice razlikuje se ovisno o osnivanju puta, podrijetlu i broju osnivača, događajima, položaju, dužini izolacije i povijesnim promjenama u broju stanovnika. Sve su to karakteristike za koje se očekuje da će

utjecati na stupanj genetske diferencijacije i obrazac specifične ravnoteže, a sve preko utjecaja na slučajna genetička skretanja, razinu endogamije i srođivanje (247).

Izoliranost populacije otoka Visa vidi se i u studiji Jerončić, 2016 (121) koja je sekvencionirala cijeli egzom 176 ispitanika s područja Visa i usporedila ga s genomom kontrole skupine s područja Škotske. Od navedenog broja 115 ispitanika kategorizirani su kao homozigotni s mutacijom specifičnih gena od kojih većina kodira enzime ili zahvaća signalne puteve. Ovaj rad potvrđuje izolirani status viške populacije. U radu se navodi još niz genetičkih specifičnosti ove populacije za koji autori smatraju da pojedine mutacije dovode do gubitka funkcije i intrigantne su u smislu adaptivne evolucije. Pružanjem relativno velikog broja varijanti koje nisu viđene drugdje, ova studija služi kao vrijedan resurs u razumijevanju ljudskih varijacija, osobito u u svjetlu genetičkih studija o ljudskim bolestima, populacijskoj genetici i evoluciji u ovoj populaciji.

Velika studija na 3 215 ispitanika odrasle dobi iz Rotterdama (239) proučavala je odnos asimetrije lica, s genetskom varijacijom na 102 lokusa polimorfizma pojedinačnih nukleotida (SNP) koje se povezuju s facijalnom varijacijom oblika. Također je ispitala negativnu povezanost stupnja individualne heterozigotnosti s facijalnom asimetrijom. Studija nije identificirala niti jedan SNP koji se odnosi na fluktuacijsku ili ukupnu asimetriju. Kao mogući razlog autori navode utjecaj relativno malog stupnja inbreedinga i relativno stabilno okruženje tijekom rasta u Rotterdamu. Rezultati ovog istraživanja u skladu su s nalazima Rotterdamskog: nema statistički značajne razlike u iznosu totalne i fluktuacijske asimetrije u endogamnoj otočnoj populaciji (Korčula, Vis), niti u miješanoj gradskoj populaciji grada Splita, iako studija Polašek, 2010 (152) koja je na četiri najčešće korištene metode i istražila polimorfizam pojedinačnih nukleotida (SNP) otočne populacije jasno ukazuje na izraženu homozigotnost ove populacije.

Kao i ovo, većina prethodnih istraživanja o genetskim aspektima asimetrije lica i zuba temelji se na usporedbi endogamne, često izolirane populacije s više egzogamnih (232, 248, 249). Stupanj heterozigotnosti povećava se s razinom egzogamije i epidemije (250) povezuje se s nižim razinama organizacijske asimetrije te odražava povećanu sposobnost ublažavanja genetskih i okolišnih stresora. Što je viši stupanj heterozigotnosti kod gena koji kodiraju proteine ili na povezanim lokusima (neslučajna asocijacija), bolje prilagođeni pojedinac štiti se od poremećaja. U tom kontekstu, predlažu se tri hipotetska mehanizma: 1) efekt „izravnog učinka“ prema kojem heterozigotnost povećava sposobnost multilokusa i može rezultirati

funkcionalnom dominacijom na lokusu *per se* (251, 252). Moguće je također da heterozigoti posjeduju enzime s različitim katalitičkim svojstvima i stoga su biokemijski učinkovitiji od homozigota (253). 2) „hipoteza lokalnog učinka“ predlaže heterozigotnost kao dodatnu dominaciju kada postoji genetska povezanost (neravnoteža povezivanja) između neutralnog markera i markera pod selekcijom (251, 254). I 3) hipoteza „općeg učinka“ navodi da je prednost heterozigota da su markeri koji se detektiraju, a koji proizlaze iz interakcije homozigotnosti, lokusi raspoređeni po cijelom genomu. Preduvjet za to je da su marker i lokusi u službi neravnoteže identiteta što se bilježi kao koeficijent inbreedinga pojedinaca. Veći koeficijent inbreedinga znači veću homozigotnost markera i sposobnost vezivanja za lokus, dok se niži koeficijent povezuje s heterozigotnosti i slabijoj povezanosti markerima i lokusa (255, 256). Kako je visok stupanj inbreedinga ispitanika ove populacije pokazan u nekoliko istraživanja u sklopu Projekta, a kako se asimetrija lica ne može povezati sa srođivanjem, mišljenja sam da se korelacija heterozigotnost - sposobnost lokusa u ovom istraživanju ne može objasniti ovim trima modelima i da zahtijeva dodatnu identifikaciju. Isti je primjer s Rotterdamskom studijom. Jedno od mogućih objašnjenja je Chapman i sur. koji su pokazali da čak i ako postoje korelacije heterozigotnost - sposobnost vezivanja za lokus, one su vrlo male (obično manje od 1 % fenotipske varijance) (255). Nadalje, stupanj heterozigotnosti može biti, u prosjeku, nedovoljno nizak da bi značajno utjecao na razvojne putove. Također je razumno pretpostaviti da okolina otočke populacije ne fluktuira dovoljno da bi homozigotnost bila nepovoljna. Treći razlog odnosi se na relativni genetski učinak na asimetriju lica u usporedbi s okolišnim stresorima koji se akumuliraju tijekom vremena.

Bit će potrebni dodatni individualni podaci o povijesti života ispitanika ovog istraživanja kako bi se dodatno istražilo ovo pitanje i moguće interakcije između genetskih i sastavnica okoliša. Očito je da se gore navedena objašnjenja međusobno ne isključuju.

U bazi podataka pronalaze se i studije u kojima se asimetrija lica povezuje sa spolom i neurokognitivnim fenotipovima s patogenetskim preklapanjem uključujući shizofreniju i autizam. Asimetrija lica varira s kognicijom u ovisnosti o spolu (257), ali se i spolno specifična asimetrija lica pojavljuje kod shizofrenije (258) i u tom slučaju povezuje se i sa specifičnim fenotipskim entiteom asimetrije mozga (259). U skladu s tim, radna skupina koja je sudjelovala u ovom Projektu ima u planu na promatranoj skupini ovog istraživanja ispitati moguću povezanost asimetrije s kognitivnim statusom budući da u bazi podataka u sklopu Projekta postoje rezultati testova inteligencije za svakog ispitanika.

6. ZAKLJUČCI

Zaključci ovog istraživanja su:

1. Totalna asimetrija cijelog kraniofacijalnog skeleta izražena u Prokrustovim jedinicama ne grupira se ovisno o dobi.
2. Totalna asimetrija cijelog kraniofacijalnog skeleta izražena u Prokrustovim jedinicama ne grupira se ovisno o spolu.
3. Totalna asimetrija kranija izražena u Prokrustovim jedinicama ne grupira se ovisno o dobi.
4. Totalna asimetrija kranija izražena u Prokrustovim jedinicama ne grupira se ovisno o spolu.
5. Totalna asimetrija mandibule izražena u Prokrustovim jedinicama ne grupira se ovisno o dobi.
6. Totalna asimetrija mandibule izražena u Prokrustovim jedinicama ne grupira se ovisno o spolu.
7. Ispitanici s područja Splita imaju najviše srednje odstupanje za totalnu asimetriju cijelog kraniofacijalnog skeleta, dok ispitanici s područja Visa imaju najviše vrijednosti.
8. Ispitanici s područja Splita imaju najviše srednje vrijednosti, ali i najviše srednje odstupanje za totalnu asimetriju za područje kranija.
9. Ispitanici s područja Visa imaju najviše srednje vrijednosti, a najviše srednje odstupanje za totalnu asimetriju, područje mandibule pokazuju ispitanici s područja Korčule. Ispitanici s područja Korčule statistički se razlikuju u iznosu totalne asimetrije za područje mandibule u odnosu na ispitanike Visa i Splita.
10. Nema statistički značajne razlike u iznosu totalne asimetrije za cijelo područje kraniofacijalnog skeleta ovisno o iznosu srođivanja.
11. Nema statistički značajne razlike u iznosu totalne asimetrije za cijelo područje kraniofacijalnog skeleta ovisno o dobi.
12. Nema statistički značajne razlike u iznosu totalne asimetrije za cijelo područje kraniofacijalnog skeleta ovisno o spolu.
13. Nema statistički značajne razlike u iznosu totalne asimetrije za cijelo područje kraniofacijalnog skeleta ovisno o mjestu stanovanja (Korčula, Split, Vis).
14. Nema statistički značajne razlike u iznosu totalne asimetrije za područje mandibule ovisno o iznosu srođivanja.

15. Nema statistički značajne razlike u iznosu totalne asimetrije za područje mandibule ovisno o dobi.
16. Nema statistički značajne razlike u iznosu totalne asimetrije za područje mandibule kraniofacijalnog skeleta ovisno o spolu.
17. Nema statistički značajne razlike u iznosu totalne asimetrije za područje kranija ovisno o iznosu srođivanja.
18. Nema statistički značajne razlike u iznosu totalne asimetrije za područje kranija ovisno o dobi.
19. Nema statistički značajne razlike u iznosu totalne asimetrije za područje kranija ovisno o spolu.
20. Iznosi za totalnu asimetriju općenito znatno su veći za područje manidbule, nego za područje kranija i za totalnu asimetriju.
21. Postoji direkcijska asimetrija cijelog kraniofacijalnog skeleta kod svih triju skupina ispitanika. Nema statistički značajne razlike u iznosu direkcijske asimetrije cijelog kraniofacijalnog skeleta između skupina ispitanika s područja Korčule, Visa i Splita. Ispitanici s područja Visa imaju najveći iznos direkcijske asimetrije za cijelo područje kraniofacijalnog skeleta.
22. Postoji direkcijska asimetrija kranija u svim trima skupinama ispitanika. Nema statistički značajne razlike u iznosu direkcijske asimetrije kranija između skupina ispitanika s područja Korčule, Visa i Splita. Ispitanici s područja Visa imaju najveći iznos direkcijske asimetrije za područje kranija.
23. Postoji direkcijska asimetrija manidbule u svim trima skupinama ispitanika. Nema statistički značajne razlike u iznosu direkcijske asimetrije za područje mandibule između skupina ispitanika s područja Korčule, Visa i Splita. Ispitanici s područja Korčule imaju najveći iznos direkcijske asimetrije mandibule. Iznos direkcijske asimetrije najmanji je za mandibulu za sve tri skupine ispitanika.
24. Vektorska analiza direkcijske asimetrije pokazala je veće promjene na orbitalnom i nazalnom području kod svih triju skupina (Korčula, Split, Vis), dok su promjene na području mandibule zamjetljivo male. Nema značajno različitih promjena direkcijske asimetrije s dobi.
25. Postoji fluktuacijska asimetrija cijelog kraniofacijalnog skeleta u svim trima skupinama ispitanika (Korčula, Vis, Split). Nema statistički značajne razlike u iznosu

fluktuacijske asimetrije cijelog kraniofacijalnog skeleta između skupina ispitanika s područja Korčule, Visa i Splita.

26. Postoji fluktuacijska asimetrija kranija u svim trima skupinama ispitanika (Korčula, Vis, Split). Nema statistički značajne razlike u iznosu fluktuacijske asimetrije cijelog kraniofacijalnog skeleta između skupina ispitanika s područja Korčule, Visa i Splita. Srednja vrijednost fluktuacijske asimetrija kranija, kao i srednje odstupanje, najveće je za ispitanike s područja Visa. Iznosi fluktuacijske asimetrije za područje kranija veći su od fluktuacijske asimetrije mandibule.
27. Postoji fluktuacijska asimetrija mandibule u svim trima skupinama ispitanika (Korčula, Vis, Split). Nema statistički značajne razlike u iznosu fluktuacijske asimetrije cijelog kraniofacijalnog skeleta između skupina ispitanika s područja Korčule, Visa i Splita. Srednja vrijednost fluktuacijske asimetrija mandibule, kao i srednje odstupanje, najveće je za ispitanike s područja Splita. Iznosi fluktuacijske asimetrije za područje mandibule manji su i od fluktuacijske asimetrije kranija.
28. Nema statistički značajne razlike u iznosu fluktuacijske asimetrije u odnosu na dob.
29. Nema statistički značajne razlike u iznosu fluktuacijske asimetrije u odnosu na spol.
30. Nema statistički značajne razlike u iznosu fluktuacijske asimetrije u odnosu na iznos srođivanja.
31. Vektorskom analizom smjera fluktuacijske asimetrije u odnosu na dob vidi se kako su promjene smjera izraženije u skupini ispitanika starijih od 55 godina i to dominantno u nazo-orbitalnom području.
32. Između ispitanika ženskog i muškog spola postoji statistički značajna razlika u obliku kraniofacijalnog skeleta.
33. Dobne promjene oblika kraniofacijalnog skeleta veće su kod ispitanika ženskog, nego kod ispitanika muškog spola. Dobne promjene u obliku kraniofacijalnog skeleta imaju stalnu uzlaznu promjenu, no nakon 55 godina krivulja promjene oblika kraniofacijalnog skeleta u ovisnosti o dobi kod ispitanika ženskog spola postaje diskontinuirana s nepredvidljivim uzlaznim i silaznim varijacijama. Promjene oblika kraniofacijalnog skeleta između ispitanika ženskog i muškog spola do 55. godine statistički se razlikuju, ali se ta značajnost nakon 55. godine gubi.
34. Ispitanici se promjenom oblika kraniofacijalnog skeleta s obzirom na mjesto stanovanja (Korčula, Split, Vis) ne grupiraju u klastere. Postoji statistički značajna razlika između ispitanika Korčule i Visa u obliku kraniofacijalnog skeleta.

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8. PRILOZI I SKRAĆENICE

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SKRAĆENICE:

ap - apertura piriformis

CBCT - cone beam kompjuterizirana tomografija

cn - coronoid

CNN - connected cellular network

CNS - centralni nervni sustav

CT - kompjuterizirana tomografija

DA - direkcijska asimetrija

DICOM - digital imaging and communication in medicine

DNA - deoksiribonukleinska kiselina

FA - fluktuacijska asimetrija

fi - foramen incisivus

fma - foramen mandibule

fme - foramen mentale

FOV - field of view

HPLC - high performance liquid chromatography

id - infradentale

IUŽ - intrauterinog života

lng - linguale

MLH - mulitilocus heterozygosity

MR - magnetska rezonanca

mt DNA - mitohondrijska deoksiribonukelinska kiselina

or - orbitale

PCA - Principal Components Analy*sis*

pr - prosthion

RNA - ribonukleinska kiselina

ROI - regio of interest

sna - spina nasalis anterior

snp - spina nasalis posterior

TA - totalna asimetrija

TFM - teorija funkcijskog matriksa

VNTR - Variable number tandem repeat

zm - zygomaxillare

zo - zygoorbitale

μCT - mikro kompjuterizirana tomografija

Životopis

Ivana Rupić rođena je u Šibeniku gdje je završila osnovno i srednjoškolsko obrazovanje. 2006. godine upisala je Stomatološki fakultet u Zagrebu kojeg je apsolvirala 2013. godine, a 2019. godine stječe i titulu specijalist ortodoncije. Tijekom studija započela se baviti znanstvenim radom i 2012. godine dobila Rektorovu nagradu za rad "Procjena učinkovitosti diodnog lasera na postoperativnu kvalitetu života nakon kirurškog uklanjanja trećih donjih molara". Autor je više znanstvenih radova iz područja dentalne radiologije i zaštite od zračenja publiciranih u međunarodnim znanstvenim časopisima koji se citiraju u CC i SCI bazi. Aktivni je sudionik i član organizacijskog odbora više znanstvenih simpozija i stručnih skupova. Aktivni je član EADMFR-a (European Academy of Dento Maxillo Facial Radiology) te je u veljači 2019. godine sudjelovala na 6. Junior Meetingu EADFMR-a.

Od 2013. godine zaposlena je u Stomatološkoj poliklinici Apolonija kao ortodont, voditelj 3D dijagnostike i stručni suradnik Zubnog rendgena dr. Lauc za kontrolu kvalitete rendgenskih snimaka i zaštitu od zračenja. Znanstveno se višemjesečno usavršavala 2014. godine u Zavodu za antropologiju Sveučilišta u Beču, gdje se bavila geometrijskom morfometrijom i 3D morfološkom analizom antropometrijskih obilježja. Od tada do danas svake godine u sklopu izrade doktorata studijski boravi na Zavodu za antropologiju Sveučilišta u Beču.

Aktivno sudjeluje u pripremi predavanja iz područja kraniofacijalne morfologije unutar kolegija "Dentalna antropologija" na Studiju antropologije Filozofskog fakulteta u Zagrebu. Suradnica je u nastavi poslijediplomskog specijalističkog studija "Dentalna implantologija" na Stomatološkom fakultetu u Zagrebu. Autorica je i koautorica poglavlja "Označavanje zuba", "Metode slikovnih prikaza orofacijalnih struktura" i "Epidemiologija orofacijalnih bolesti" u knjizi "Dentalna antropologija" koja je u pripremi za tisak (autori Lauc T., Čuković-Bagić I. i sur.). U istoj knjizi prevela je s engleskog jezika i obradila poglavlje "Kontrolni čimbenici kranijalne morfogeneze i teorijska tumačenja", autora Alberta Caprioglia. U suradnji sa Stomatološkim fakultetom Sveučilišta u Sarajevu, na Katedri za ortodonciju, sudjeluje u međunarodnom istraživanju koje obuhvaća kefalometrijska mjerenja i mjerenja vratnih kralježaka populacije u dobi od 7-15 godina te sudjeluje u istraživanjima CBCT dijagnostike.

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Page 6 Results

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Page 10 Results

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Page 11 Results

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Page 16 Results

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Page 31 Results

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Page 34 Results

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Page 35 Results

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Page 36 Results

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Page 40 Results

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Page 82 Results

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Page 113 Results

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Page 114 Results

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Page 140 Results

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Page 142 Results

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Page 143 Results

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Page 144 Results

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Page 147 Results

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Page 148 Results

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Page 149 Results

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Page 150 Results

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Page 151 Results

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Page 152 Results

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Page 154 Results

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Page 161 Results

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Page 162 Results

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Page 165 Results

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Page 166 Results

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Page 166 Results (contd.)

(X) Font Times New Roman,Bold is not embedded. Font Times New Roman,Bold can not be embedded because: Could not find matching font to embed
(X) Font Times New Roman,Bold is not embedded. Font Times New Roman,Bold can not be embedded because: Could not find matching font to embed
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(X) Font Times New Roman is not embedded. Font Times New Roman can not be embedded because: Could not find matching font to embed - 14 more not displayed

Page 167 Results

(X) Font Times New Roman,Italic is not embedded. Font Times New Roman,Italic can not be embedded because: Could not find matching font to embed
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Page 168 Results

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(X) Font Times New Roman,Italic is not embedded. Font Times New Roman,Italic can not be embedded because: Could not find matching font to embed
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Page 169 Results

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Page 170 Results

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Page 171 Results

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