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Hominization tendencies in the evolution of primates in multidimensional modeling

Abstract The evolutionary radiation of primates determined many developmental paths among which there is a hominization tendency that leads to the emergence of the modern human. This evolution was studied on the basis of the measurements defining Morant and Sergi's index [21], which were taken on 68 skulls of chosen adult monkeys, apes and fossil hominids. They were classified into 10 separate taxons. The skull measurements were analyzed with the help of the following methods: descriptive statistics and discriminant analysis, a method that enables spotting differences between the taxons studied on the basis of Mahalanobis distance. Moreover, analysis of variance, ANOVA, was applied as well as Tukey's multiple comparisons and Kendall's τ rank correlation coefficient based on the difference in the probability of growth or decrease in one variable in relation to another one. As a result, the analysis performed showed that apes originate from the primitive forms related to the chimpanzee (*PAN* taxon) and orangutan (*PONGO* taxon). The evolution of the baboon (*PAPIO* taxon) branched off to form the line leading to humans at the orangutan (*PONGO* taxon). Gibbons are forms which differ from their evolutionary roots the most. Hominids, through their massive and gracile *Australopithecus* forms, led simultaneously to the emergence of *Pithecanthropus*, whose further evolution resulted in the neanderthal form. Modern humans have remained distinct from other primates due to simultaneous growth of cranial vault and height, which allowed for considerable brain development. This type of development can be regarded as a manifestation of a qualitative jump in the evolution of primates.

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1. Introduction Evolutionary radiation of primates is based on three main paradigms: 1. the irreversibility of evolutionary processes; 2. the principle according to which too highly specialized forms represent closed developmental paths and are not capable of abrupt qualitative changes; 3. small cumulative quantitative changes can only cause better adaptation to environmental conditions. However, if these conditions change, the whole system is destroyed. It seems that the paradigms mentioned above determine many

developmental paths of primates, including the one which has been preoccupying human creative thinking for centuries and is called the hominization tendency, that is the line leading to the rise of Homo sapiens. It has been noticed in anthropological sciences that among primates leading to the Homo genus young forms have a relatively bigger cranium than older ones [20]. Moreover, sexual dimorphism of the skull varies according to species and is expressed in apes, among other things, in better developed canines in the case of males than in the case of females, [27]. Evolution of primates, by creating radiation adaptations and being the result of adaptation to different environments, has led to the emergence of Homo sapiens. Such features of the modern human, such as brain development, with perception centres for impulses coming from his natural environment and ability to stimulate them according to his own needs, can be observed independently in many lineages of primates [7]. Recently, Hennenberg and Saniotis [9] studied the evolutionary origins of the human brain; Blažek, Brużek and Casanova [1] described the relation between changes in brain structures and brain size in human evolution. According to Pilbeam [18], the evolution of the axial pattern in primates reflects phylogenetic relationships. Cercopithecidae monkeys show less similarity within and between species than hominids. Moreover, great apes could not be considered as ancestral to humans. Gibbons form a group presenting an adaptative radiation to highly arboreal, acrobatic and swinging forms, showing no similarity to the hominids including Homo Sapiens. Niemitz [16], proved upright posture to be the main factor in hominid evolution. The evolution of upright posture is another feature which enables bipedal locomotion and is expressed in the connection of the skull to the vertebral column at a 90 degree angle. This causes a forward shift of the great foramen, as compared to quadrupeds whose foramen is at the back of the head [22]. So, the hominization tendencies of primates can be studied on the basis of the direct skull measurements determining Morant and Sergi's index [21], as well as on the basis of the index itself, defining the relative size of the neurocranium in relation to the viscerocranium. The size of this index is inversely proportional to the relative size of the neurocranium. Taking into consideration the arguments above, we would like to apply multidimensional modelling which helps to reveal changes in the direct skull measurements determining Morant and Sergi's index [21]. The point is that we want to present, on a plane, projections of multidimensional connections, [5] and [15], the analyzed forms of primates on the basis of the above-mentioned features. According to Singleton [23], the Mahalanobis distance matrix shows the phylogenetic relationship between various groups of primates. It will allow us to suggest a model of hominizing trends in primates. The aim of this work is to suggest an evolutionary model of primates based on significant differences between the studied forms belonging to established taxons. In this work we would like to compare skull measurements and the values of Morant and

Sergi's index for chosen representatives of monkeys and apes, as well as for chosen fossils of plio-pleistocene hominids. It will allow us to indicate forms leading to the emergence of the Homo sapiens skull type. The material - we are in possession of - is unique, therefore the value of each find is equivalent to a random sample taken from a population according to the principles of numerical taxonomy [24]. Moreover great apes threatened with extinction are protected animals [4].

2. Material and methods A total of 68 skulls of monkeys, apes and hominids were examined. The skulls of monkeys and apes were measured at the Museum of Natural History in Paris by Sikorska-Piwowska. The material consists of: *Papio papio* – 3 skulls, *Mandrillus sphinks* – 2 skulls, *Mandrillus leucophaeus* – 2 skulls, *Hylobates lar* – 4 skulls, *Hylobates concolor* – 1 skull, *Hylobates leucoscicus* – 1 skull, *Synphalangus syndactylus* – 1 skull, *Troglodytes niger* – 6 skulls, *Pan satyrus* – 9 skulls, *Pongo pygmeus* – 5 skulls, *Gorilla gorilla* – 13 skulls. All the individuals studied had reached adult age, which should be equated with the skull reaching full morphological maturity and hence its stabilization. Adulthood was established on the basis of erup-

Table 1: Age establised according to Schultz'steeth eruption.

Legend: M1 – 1st molar, M2 – 2nd molar, M3 – 3rd molar I1 – 1st incisor, I2 – 2nd incisor, P1 – 1st premolar, P2 – 2nd premolar, C – canine teeth

Monkey age	Permanent teeth	Ape age	Code of age groups
0–1	–	0–2	0
1–2	M1	3–4–5	1
2–3	I1 I2	5–6	2
3–4	M2 P1 P2	6–7	3
4–5	C	7–8	4
5–6	–	8–9	5
6–7,8	M3	9–10,11	6
6,8-24	M3	11-40	7

tion of all permanent teeth (Table 1). This means that for monkeys the adult individuals are between 6 and 24 years old, and for apes – between 9 and 40 years old. Males and females are considered together so, that the differences between sexes do not blur taxonomic differences. This simplification is based on the general anthropological principle stating that the evolutionary tendency has blurred sexual dimorphism in the skull features. Also, of modern humans considering the phylogenetic connection of primates in different age groups confirms the hypothesis about the emergence of Homo sapiens due to retardation in the development of certain foetal features [2].The material

was grouped into the following taxons which connect appropriate genera, i.e.
Papio (*PAPIO*), Hylobates (*HYLOBATES*), Pan (*PAN*), Pongo (*PONGO*),
Gorilla (*GORILLA*). This was done on the basis of a lack of any significant
difference between the average values of skull measurements for the connected
forms using the t-Student test (Table 2). The skull measurements of the ho-

Table 2: Creation of *PAPIO*, *HYLOBATES* and *PAN* taxons in adult age
group (male and female iunctim). Factor: genus.

Taxon	Sample 1	Sample 2	Measurments	Mean1	Mean2	p–value
PAP	Papio	Mandrillus	n–ba	80.5	83.75	0.3498
	3	4	n–o	164	157.125	0.5666
			ba–pr	130.17	146.5	0.2228
			n–pr	96.17	96.25	0.9934
			MS	14.26	16.39	0.6086
HYL	Hylobates	Symphalangus	n–ba	62.42	75	
	6	1	n–o	134.08	143	
			ba–pr	72.75	104	
			n–pr	31.08	44.5	
			MS	5.46	5.06	
PAN	Pan	Troglodytes	n–ba	99.78	100.25	0.876
	9	6	n–o	21672	212.33	0.4646
			ba–pr	133.88	135.33	0.7938
			n–pr	82.44	82.83	0.9117
			MS	8.75	9.17	0.5069

minids were performed on the collection belonging to the Institute of Anthro-
pology at Cardinal Stefan Wyszynski University, by Jacek Tomczyk. All of
the casts were produced with a custom formulated high grade polyurethane
resin. They are intended for advanced graduate work or to be measured for
research purposes. The material of fossil hominids consists of three represen-
tatives of massive *Australopithecus* (KNM-ER 406; OH 5; KNW-WT 17000),
(*AUMAS* taxon), four representatives of gracile *Australopithecus* (A.L. 288-
1; Sts 5; OH 24; KNM-ER 1813), (*H.HABILIS* taxon), four representatives
of *Homo erectus* (D2700; KNM-WT 15000; KNM-ER 3733; Sangiran 17),
(*H.ERECTUS* taxon), four neanderthal forms (La Ferrasie1; La Chapelle-
aux-Saints; Atapuerca 5) (*H.HEIDELBERGENSIS* taxon), and six individ-
uals of *Homo sapiens* (Skull 5, Cro Magnon 1; Steinheim; Combe Copelle,
Predmosti III, Predmosti IV), (*H.SAPIENS* taxon). *Homo habilis* is a very
complicated species to describe. It is still debatable whether the "habilis
forms" belong to the *Homo* or *Australopithecus* genus. Because this problem
goes beyond our research, we combined gracile forms from Africa into one
taxon (*H.HABILIS*). Creation of one taxon (*H.HEIDELBERGENSIS*) from
H. heidelbergensis and *H. neanderthalensis* was connected with the similar-
ity of craniometric measurements (Table 3). The hominid representatives
did not have an obvious sex and were established to be mature. Therefore,
they could also be compared to the apes belonging to the adult age group on

Table 3: Creation of *H.HEIDELBERGENSIS* taxon from *H.Heilderbergensis* and *H.neanderthalensis.* Factor: genus.

Taxon	Sample 1	Sample 2	Measurments	Mean1	Mean2	p–value
	H.	H.	n–ba	116.5	113.5	0.8064
H.HEI	Heilderbergensis	neanderthalensis	ba–pr	83.0	83.5	0.9728
	5	4	n–pr	121.9	116.5	0.55
			n–o	356.5	357.5	0.9864
			MS	3.72	3.487	0.7812

the basis of complete eruption of permanent teeth. Developmental trends in the neurocranium and splanchnocranium were identified using Morant and Sergi's index (MS) [17], [21] and direct measurements forming this index. These measurements were taken from the 68 skulls of monkeys, apes and fossil hominids. Morant and Sergi's index was calculated according to the following formula: $MS = (100 \cdot P)/S^2$, where S is the distance n–o (25), Calot's measure of cranial vault dimension; P is the area of the upper-face triangle determined by the measurements n–ba (5), ba–pr (40), n–pr (48). The number of designations follow Martin and Saller [14]. These measurements are illustrated in Figure 1.   The area of the triangle is calculated according to Heron's formula: $P = \sqrt{p(p-a)(p-b)(p-c)}$, where a, b, and c are the lengths of the sides of the triangle, and $p = (a+b+c)/2$. The values of Morant and Sergi's index decrease as the sizes of the neurocranium and the dermal skull roof increase. On the basis of the averages of each group variables and selected descriptive statistics of Morant and Sergi's index, we made the following calculations and box charts presented in Figure 2. Box charts were constructed for all the taxons studied. Analysis of variance [3] was performed for each measured feature separately ($p < 0.00001$). In our paper we assume that all the observations are independent and have normal distribution with the same variance. The analysis was supplemented by Tukey's multiple comparisons [25]. Let
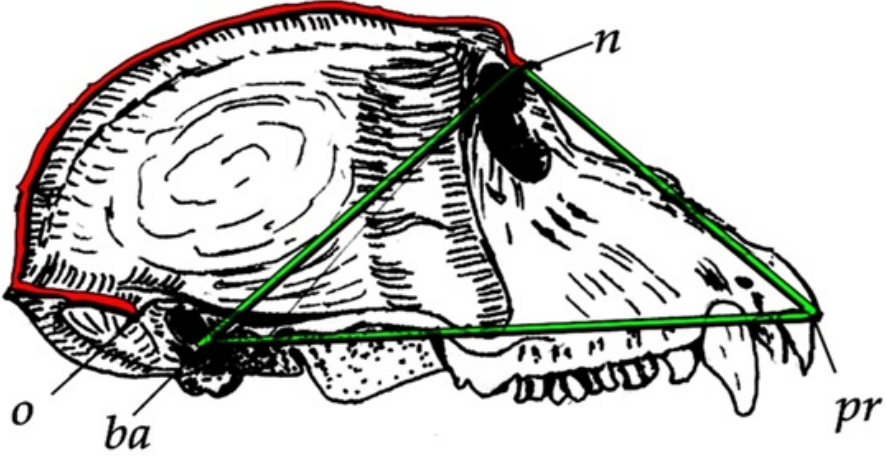
$$x_{i1}, \ldots, x_{in_i}$$

be the sample from the i-th class and

$$\bar{x}_i = \frac{1}{n_i} \sum_{l=1}^{n_i} x_{il}$$

their mean. The difference between the i-th and j-th class is considered as significant if

$$|\bar{x}_i - \bar{x}_j| \geq q_{k,n-k,1-\alpha} \sqrt{\frac{\sigma}{2}\left(\frac{1}{n_i} + \frac{1}{n_j}\right)},$$

Figure 1: A macaque skull with parameters measured using Morant and Sergi's index

Legend: ba–pr, n–ba, n–pr — upper-face triangle determined by these measurements, n–o — Callot's measure of the size of the cranial vault

where q is the quantile of the studentized-range distribution and σ^2 – within class variance is calculated according to the formula:

$$\sigma^2 = \frac{1}{n-k} \sum_{i=1}^{k} \sum_{l=1}^{n_i} (x_{il} - \bar{x}_i)^2,$$

where

$$n = \sum_{i=1}^{k} n_i.$$

Results for the *PAPIO* and *HYLOBATES* taxons are given in Table 4. Except for the n-o measurement, the rest of the features mentioned above differ considerably in these taxons. In order to combine the information obtained from one-dimensional analysis and Tukey's multiple comparisons [25], discriminant analysis was performed [28], a method which enables spotting differences between taxons on the basis of Mahalanobis distances [12]. The distances are shown in Table 5 and were calculated according to the following formula:

$$d(\bar{x}_i, \bar{x}_j) = \sqrt{(\bar{x}_i - \bar{x}_j)^{\top} S^{-1} (\bar{x}_i - \bar{x}_j)},$$

Figure 2: A Box-and Whisker plots for Morant and Sergi's index
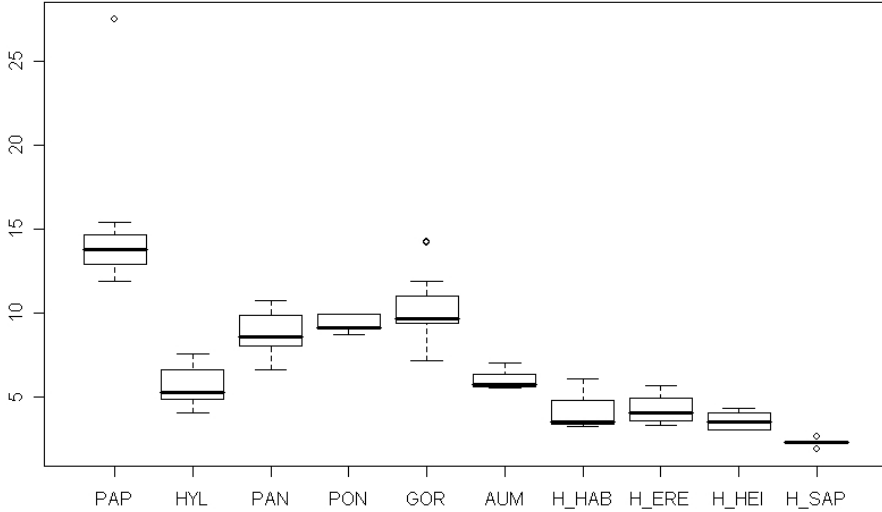
Table 4: Tukey's multiple comparisons for PAP (*PAPIO*) and HYL (*HY-LOBATES*) taxons for all the measurments and Morant and Sergi's index (MS).

Legend: Diff – difference, Lwd – lower 0.95 confidence interval, Upr – upper 0.95 confidence interval, p-significance level.

heightTaxon	Feature	Diff 1	Lwr	Upr	p
HYL–PAP	MS	-9.77	-13.56	-5.97	0.0000
HYL–PAP	n–ba	-18.14	-33.64	-2.64	0.0102
HYL–PAP	ba–pr	-62.29	-86.96	-37.61	0.0000
HYL–PAP	n–pr	-63.21	-79.87	-4656	0.0000
HYL–PAP	n–o	-24.71	-62.36	12.936	0.4951

where

$$S = \frac{1}{n-k} \sum_{i=1}^{k} \sum_{l=1}^{n_i} (x_{il} - \bar{x}_i)(x_{il} - \bar{x}_i)^{\top}.$$

Significance levels for the Mahalanobis distances were adjusted to account for multiple comparisons [13]. Using discriminant analysis the four–dimensional space defined by the direct skull measurements without the MS index was reduced to two dimensions, in order to graphically present the analyzed relations. Figure 3 shows projections of four–dimensional points corresponding

Table 5: Mahalanobis distances between the taxons studied.

Legend: PAP (*PAPIO*), HYL (*HYLOBATES*), PON (*PONGO*), GOR (*GO-RILLA*), AUM (*AUMAS*), H.HAB (*H.HABILIS*), H.ERE (*H.ERECTUS*), H.HEI (*H.HEIDELBERGENSIS*), H.SAP (*H.SAPIENS*).

|	PAP	HYL	PAN	PON	GOR	AUM	H.HAB	H.ERE	H.HEI	H.SAP
PAP	0.00	7.32	4.02	2.59	3.57	10.45	9.50	11.11	13.38	14.92
HYL	7.32	0.00	5.92	6.23	9.03	13.85	11.20	12.88	14.96	16.00
PAN	4.02	5.92	0.00	1.69	3.20	10.01	8.66	9.64	11.54	13.17
PON	2.59	6.23	1.69	0.00	3.88	10.13	8.79	10.09	12.12	13.56
GOR	5.37	9.03	3.20	3.88	0.00	9.37	9.27	9.46	10.98	13.05
AUM	10.45	13.85	10.01	10.13	9.37	0.00	3.94	3.22	5.07	7.47
H.HAB	9.50	11.20	8.66	8.79	9.27	3.94	0.00	2.86	5.40	6.61
H.ERE	11.11	12.88	9.64	10.09	9.46	3.22	2.86	0.00	2.77	5.17
H.HEI	13.38	14.96	11.54	12.12	10.98	5.07	5.40	2.77	0.00	3.52
H.SAP	14.92	16.00	13.17	13.56	13.05	7.47	6.61	5.17	3.52	0.00

to skulls in the sample onto the two-dimensional subspace spanned by the two first canonical directions.

Figure 3: Discriminant analysis of the taxons studied
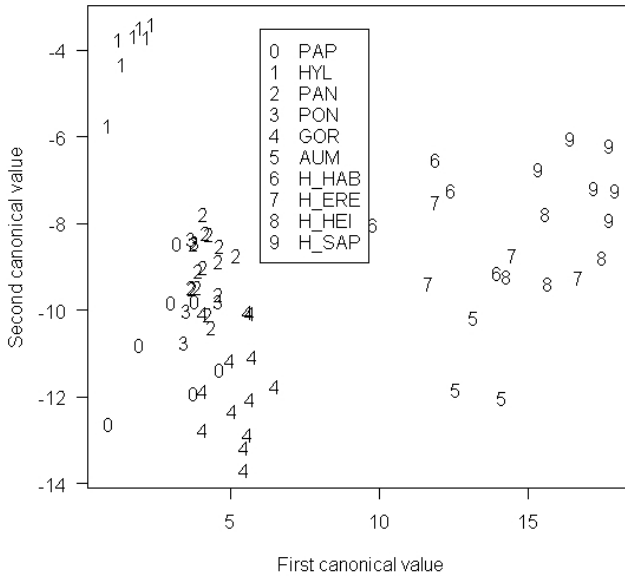
By definition [11], the i–th canonical direction is the eigenvector corre-

Figure 4: Correlation coefficients, according to Kendall, concerning direct measurements of primates studied
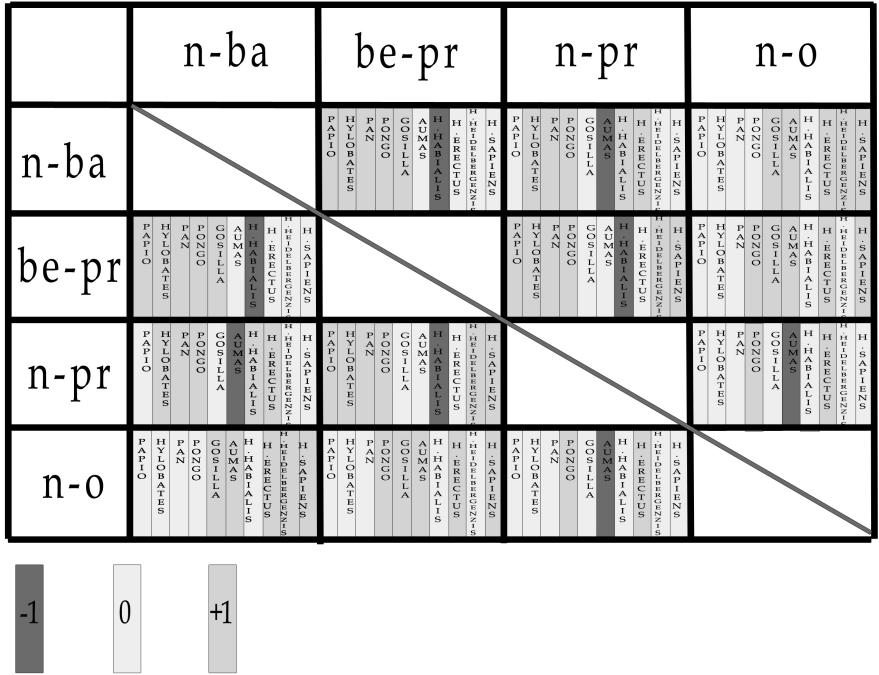
sponding to the i–th largest eigenvalue, where S and B are the within–class and between–class variance–covariance matrices, respectively. If

$$x_{i1}, \ldots, x_{in_i}$$

is the sample from the i–th class (in our case–taxon) then:

$$S = \frac{1}{n-k} \sum_{i=1}^{k} \sum_{l=1}^{n_i} (x_{il} - \bar{x}_i)(x_{il} - \bar{x}_i)^\top,$$

$$B = \frac{1}{k-1} \sum_{i=1}^{k} n_i (\bar{x}_i - \bar{x})(\bar{x}_i - \bar{x})^\top,$$

$$\bar{x}_i = \frac{1}{n_i} \sum_{l=1}^{n_i} x_{il}, \qquad \bar{x} = \frac{1}{n} \sum_{i=1}^{k} n_i \bar{x}_i.$$

The work was based on Mahalanobis distances–objective measurements for multi-dimensional analysis. From a mathematical point of view, this method changes the coordinate system in such a way as to make the autocovariance matrix a unit matrix. This means that this method minimizes the influence of variability within taxons and so aids spotting the most significant differences between them. Rank correlation coefficients [10] were also applied in our research. Such coefficients only use orderings of objects in terms of the size of particular features. Kendall's τ coefficient based on ranks is a measure of the correlation of two ordinal level variables. The correlation between pairs of direct skull measurements for the primates studied was expressed with the help of this coefficient (Figure 4). The rank correlation coefficient was calculated according to the following definition: Let $(x_1, y_1)(x_2, y_2), \ldots, (x_n, \ y_n)$ be a set of observations of the random variables X and Y, such that all the values of x_i and y_i are unique. Any pair of observations $(x_i, \ y_i)$ and $(x_j, \ y_j)$ are said to be concordant if the ranks of both elements agree: that is, if both $x_i \ > \ x_j$ and $y_i \ > \ y_j$ or if both $x_i \ < \ x_j$ and $y_i \ < \ y_j$. They are said to be discordant, if $x_i \ > \ x_j$ and $y_i \ < \ y_j$ or if $x_i \ < \ x_j$ and $y_i \ > \ y_j$. If $x_i \ = \ x_j$ or $y_i \ = \ y_j$, the pair is neither concordant nor discordant. The Kendall τ coefficient is defined as:

$$\tau = \frac{(\text{number of concordant pairs}) - (\text{number of discordant pairs})}{n(n-1)/2}.$$

All the statistical calculations were performed using the R computing package [19].

3. Results Mahalanobis distances were used to determine morphological similarities between the primates studied. These similarities allowed us to construct a model describing the tendencies in skull evolution which led to the Homo sapiens form. This is shown on the graph (Figure 5), where particular nodes correspond to the analyzed taxons. Here, each taxon represents a separate form whose evolution took place independently, and the distances between them shed light on the relationship between the groups presented. This research is supplemented by a multilateral connection graph (Figure 6). In this graph the primates studied are divided into two polyphyletic different groups – monkeys with apes, and hominids. Moreover, hominids are closest to gorillas (*GORILLA* taxon). According to Groves [8], humans constitute a sister group to gorillas. Within monkeys and apes, the most distinct form from their evolutionary root is the gibbon (*HYLOBATES* taxon), whilst apes originate from primitive forms related to the chimpanzee (*PAN* taxon) and orangutan (*PONGO* taxon). Evolution of the baboon (*PAPIO* taxon) branched off from the line leading to humans at the orangutan (*PONGO* taxon). Hominids, both massive (*AUMAS* taxon) and gracile (*H.HABILIS* taxon), have independently evolved towards developing *Pithecanthropus* features (*H.ERECTUS* taxon). In *Pithecanthropus* forms, hominization evolved

Figure 5: Graph of distances between the taxons
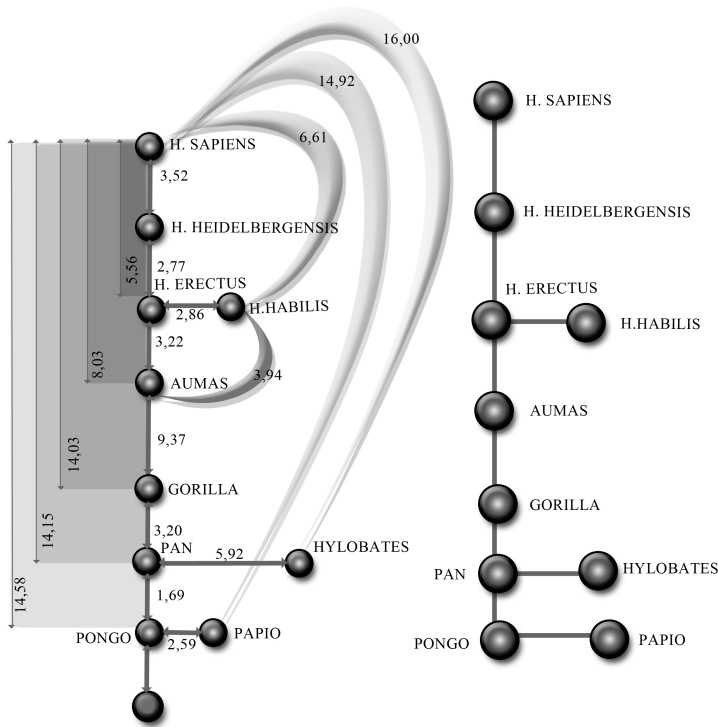
towards neanderthal forms (*H.HEIDELBERGENSIS* taxon) and with them the evolution of these taxa finishes. This was proved by Krings' genetic research in 2003 (c.f. [6]). According to Volpoff [26], the lineages leading to neanderthals and Homo sapiens are completely separate. The modern human (*H.SAPIENS* taxon) has inherited features of all the primates, while remaining at the same time distinct from them, due to the fact that both the height of the skull (n–ba measurement) and its vault increased (n–o measurement) (Figure 4). Kendall's τ coefficient, presented in this figure, also indicates the diversity of the forms calculated on the basis of the Mahalanobis distance.

Figure 6: Graph of multilateral connections within the groups of the taxons studied
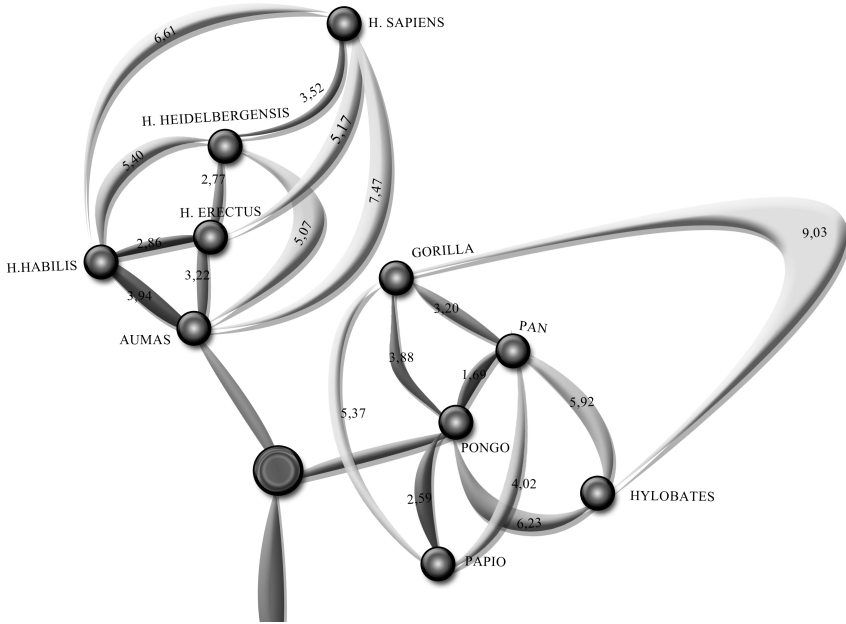
4. Conclusions

The study presented here makes it possible to formulate a few suggestions on understanding anthropogenesis.

- Primate evolution is polyphyletic.

- Within primates, there is a general tendency towards the emergence of Homo sapiens which ends, however, with the neanderthal form, due to irreversibility of evolution.

- Massive ($AUMAS$) and slender, or gracile, ($H.HABILIS$) australopitheci lead independently to the emergence of *Pithecanthropus* ($H.ERECTUS$), whose further evolution resulted in the neanderthal form.

The phenomenon of the origin of *Homo sapiens*, that is of the modern human, is a manifestation of a qualitative jump in primate evolution. Growth of the vault and height of the cranium correlated with the development of the brain and its centers enabling abstract and creative thinking. According to Aristotle, this is a purely human feature connected with a thirst for knowledge in itself. To give a biological explanation of this phenomenon, it can be supposed that during evolution the skull of an adult human has become

similar to earlier and earlier stages of his ontogenetic development [2].

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Tendencje hominizacyjne ewolucji naczelnych w wielowymiarowym modelowaniu

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Streszczenie Radiacja ewolucyjna naczelnych wyznaczyła wiele dróg rozwojowych a wśród nich tendencję hominizacyjną prowadzącą do powstania człowieka współczesnego. Ta ewolucja została zbadana na podstawie pomiarów tworzących wskaźnik Moranta i Sergiego [14], pobranych na 68 czaszkach wybranych małp i kopalnych hominidów w wieku adultus. Zostały one zakwalifikwane do dziesięciu odrębnych taksonów. Pomiary czaszek zostały opracowane przy użyciu statystyki opisowej i analizy dyskryminacyjnej, jako metody pozwalającej na wychwycenie różnic między badanymi taksonami co zostało przedstawione na podstawie odległości Mahalanobisa. Ponadto zastosowano analizę wariancji ANOVA wraz z porównaniami wielokrotnymi Tukeya oraz rangowy współczynnik korelacji τ Kendalla oparty na różnicy prawdopodobieństwa wzrostu lub zmniejszania się jednej zmiennej pomiarowej względem drugiej. W wyniku przeprowadzonych analiz stwierdzono, że ewolucja małp człekokształtnych przebiegała od form prymitywnych, których cechy czaszki nawiązywały do zbadanych przez nas form taksonów szympansa i orangutana, a formą najbardziej odbiegającą od rdzenia ich ewolucji jest gibon. Ewolucja pawianów będzie odpowiednikiem rozwoju filogenetycznego form pośrednich prowadzących do formy orangutana. Tak więc cechy czaszki orangutana mają charakter preadaptywny, stanowiący punkt wyjścia zarówno dla małp człekokształtnych jak i zwierzokształtnych. Hominidy poprzez formy australopiteków masywnych i gracylnych doprowadziły równolegle do powstania pitekantropa, którego dalszy rozwój zaowocował w formie neandertalskiej. Człowiek współczesny pozostał odległy od wszystkich naczelnych poprzez równoczesny wzrost wysklepienia i wysokości mózgoczaszki, co pozwoliło na ogromny rozwój mózgu. Ten typ rozwoju jest wyrazem skoku jakościowego w ewolucji naczelnych.

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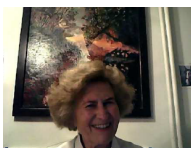
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