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Morphological evolution of formalized taxa for some monkey and ape species

Abstract The aim of this work is to present taxa which link various species and genera according to morphological stages in the development of primates. The research material consists of 115 skulls of monkeys and apes. The variability in their neurocranium and splanchnocranium ratios can be characterized by Morant and Sergi's index and by the direct measurements that define this index. Analysis of the results leads to the following conclusions: In the *PAPIO* taxon (baboons), sex dimorphism exceeds the differences between the genera. In the *PAN* taxon (chimpanzees), there are no significant differences between the genera and sexes. By studying taxonomic differences between the taxa, it can be stated that the evolutionary radiation of apes started from an initial form corresponding to the contemporary chimpanzee. Gibbons *HYLOBATES* differ equally from both baboons and great apes. In the area of the features studied, the *PONGO* taxon links to Old World monkeys. This does not mean that these taxa have a close phylogenetic relationship, but that the evolution of the *PAPIO* form may have proceeded in the direction of the great apes through a number of intermediate forms. Analysis of the rate and rhythm of skull development in the primates studied indicates that young individuals are relatively similar to each other, irrespective of taxonomic differences. Taxonomic differences are only clearly visible in the period of morphological stability.

Key words and phrases: polyphyletic development of primates; primates taxonomic differences, the variability in neuro- and viscerocranium ratios in primates.

1. Introduction

The evolution of primates has led to a set of paths characterizing developmental stages in particular species. One can observe a range of parallel developmental lines, which are reflected in the skull morphology of contemporary monkeys and apes [23]. This study presents a model based on taxonomic skull features that correspond to the genotype as revealed by the phenotype. This is combined with an attempt to link the accumulated knowledge on the evolution of primates with a categorization of the species surveyed based on

groups of characteristics. These groups of features are interpreted as a set of points in space, where each trait is assigned to one axis. This will enable the construction of an evolutionary tree illustrating the similarity of the morphological development of skull characteristics in these species. Such an approach requires a far-reaching formalization concerning both the systematics and the origin of the monkeys and apes studied.

According to Hennig [10], phylogenetic origin can be studied on the basis of present forms which possess features adaptive to the conditions they live in. These are so-called apomorphic features. Formalization of primate systematics consists of the defining taxa which group particular species or genera together on the basis of a lack of significant differences in the features studied. The features considered are the development of the neurocranium and viscerocranium, which give information regarding the distances between the different forms observed at present, which can be described in the form of an evolutionary tree. This corresponds to Hennig's idea [10] according to which the closer the groups compared are inter-related, the larger the number of similar features they have [1]. For example, according to Groves [8], gorillas constitute a sister group to humans.

This approach is based on creating primate taxa that group individual species or genera together based on a lack of significance of the differences in the characteristics considered.

The primates studied here are monkeys represented by baboons, lesser apes represented by gibbons, and great apes represented by chimpanzees, gorillas and orangutans. The pace and rhythm of skull development in juveniles differs according to species, which affects the shape and size of the braincase and of the facial skeleton of the skull. Age can be assessed based on the presence of permanent teeth. During the period of sexual maturation in primates, the process of skull development begins to stabilize. Maturity is reached later in humans and apes than in monkeys, which is called developmental retardation [3]. For example, monkeys reach sexual maturity at the age of 4–5 years, apes — at the age of 8–11 years, whereas humans — at the age of 14–16 years.

Several studies have suggested that distinct patterns of sexual dimorphism may assist in species recognition and perhaps in phylogenetic analysis [18]. According to Plavcan [18], the observed pattern of Mahalanobis distances suggests that *Papio* represents the primitive morphometric form of African papionins, as a result of parallel evolution.

Developmental retardation is also reflected in brain weight, which increases in size starting from monkeys, to apes and ending with humans. The ability of humans to balance their head on top of their spine is possible due to the reduction in the size of their facial skeleton. According to Bolk [3], the process of hominization, i.e. the emergence of humans (*Homo sapiens*), is closely connected with the process of developmental retardation. The author

assumes that in the fetuses of all primates there is a right angle between the long axis of the head in the median sagittal plane and the longitudinal axis of the spine. In ontogenetic development, this angle changes to 180 degrees, which requires the support of four limbs. Only humans retain the right angle, which creates the necessity of a vertical posture. Otherwise, in the case of a quadrupedal posture, humans would have to look down.

This change in the position of the head, together with the fact that it balances on top of the spine, changes the nature of the perception of stimuli received from the external environment. According to Bielicki and Fiałkowski [2], this lead to the development of new centres in the cerebral cortex and to the miniaturization of neurons, as well as to the enlargement of their synapses. According to Teilhard de Chardin [27], this miniaturization of neurons means that the surface of the human cerebral cortex is the size of the dome of St Peter's Basilica, whereas the unfolded cerebral cortex of apes would cover at most the surface of an average table.

According to Ravosa and Profant [20], allometric effects might also account for homoplasies in the shape of the cranium in the species studied. Niemitz [15] proved that the occasionally upright posture of apes influenced their neurocranium development. According to Pilbeam [17], the differences between suspensory and quadrupedal primates are reflected in the vertebral column, as well as in differences in skull morphology.

The aim of this work is to present taxa which link different species and genera according to morphological stages in the development of primates with the use of a clear mathematical formalism.

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 [29].

2. Material and methods A total of 115 skulls of monkeys and apes were examined. The research material consists of

- Papio porcarius* — 2 skulls,
- Papio papio* — 11 skulls,
- Papio hamadryas* — 3 skulls,
- Papio doguera* — 1 skull,
- Mandrillus sphinx* — 6 skulls,
- Mandrillus leucophaeus* — 4 skulls,
- Hylobates lar* — 5 skulls,
- Hylobates concolor* — 2 skulls,
- Hylobates leucoscicus* — 5 skulls,
- Hylobatus pileatus* — 1 skull,
- Hylobates agilis* — 1 skull,
- Symphalangus syndactylus* — 1 skull,
- Pan troglodytes niger* — 11 skulls,
- Pan satyrus* — 28 skulls,

Pongo pygmaeus — 9 skulls,

Gorilla gorilla — 25 skulls.

These skulls were measured by Sikorska-Piwowska at the Institute of Paleontology and in the Laboratory of Comparative Anatomy in Paris, where information about their sex was also provided. This material was obtained from a museum collection dated from 1943 to 1962. At present, great apes threatened with extinction are protected [5] and it is not possible to create a similar collection now.

The ages of the apes and monkeys were defined on the basis of the presence of permanent teeth [22] and common stages of development denoted by age groups 0–7 were introduced. This is illustrated in Table 1.

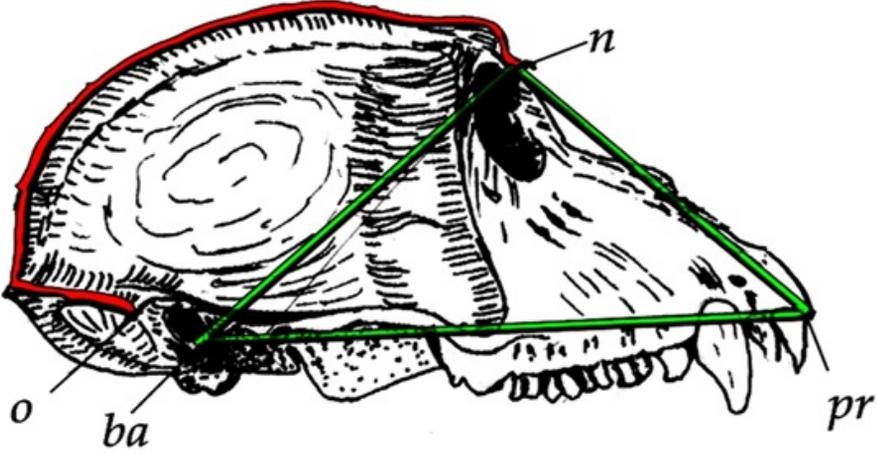
Table 1: Age established according to Schultz’s method based on the presence of permanent teeth.

Abbreviations: M1 — 1st molars, M2 — 2nd molars, M3 — 3rd molars, I1 — 1st incisors, I2 — 2nd incisors, P1 — 1st premolars, P2 — 2nd premolars, C — canine teeth.

Monkey’s age in years	Permanent teeth	Ape’s age in years	Age group
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

The introduction of common stages of development to categorize the skulls is necessary because of the later maturation of higher primates compared to monkeys [29], as well as due to the necessity of comparing their developmental paths. Measurements were made on these skulls according to an anthropometric method developed by Martin and Saller [13], which aims to compare various anthropometric features of monkeys and apes. Using this approach, each skull is described by a set of parameters based on the distances between strictly defined points on the surface of that skull. These points are named and abbreviated as follows: nasion (n), basion (ba), opisthion (o), prosthion (pr). These points and parameters are illustrated in Figure 1.

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

The variability in neurocranium and viscerocranium ratios was expressed with the help of Morant and Sergi's index [21, 25] according to the formula: $\frac{100P}{S^2}$ where: $S = n-o$ (25) — Callot's measure of the size of the cranial vault, P — the area of the upper-face triangle determined by the measured characteristics: n-ba (5), ba-pr (40), n-pr (48). The area of this 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 $p = \frac{a+b+c}{2}$ [9].

The values of Morant and Sergi's index (MS) decrease as the sizes of the neurocranium and dermal-skull roof increase. Due to the uniqueness of the research material [5], it was necessary to combine species and genera into common taxa corresponding to the sample, especially when classifying the material according to age and sex. This was done after calculating the significance of differences between direct measurements and Morant and Sergi's index in the groups with the help of the Student T-test [16]. These calculations involved the creation of *PAPIO* and *PAN* taxa. As an example, we present only one table (Table 2), showing the *PAPIO* taxon.

Table 2: Calculation of the significance of differences between the averages of direct measurements and Morant and Sergi's index in the creation of the *PAPIO* taxon

Significance: X — (5%), XX — (1%)

Genus, Taxon	Sex	Age group	Factor	Sample1 (Count)	Sample2 (Count)	Measurements	Mean 1	Mean 2	Calculated p-value	Significance					
<i>Papio, Mandrillus</i>	F, M	<i>iunctim</i>	genus	1. <i>Papio</i> F(8)	2. <i>Mandrillus</i> F(4)	n-ba	60.94	69.25	0.1616						
						n-o	154.37	154.37	1.0000						
						ba-pr	71.87	100.62	0.0270	X					
						n-pr	49.87	67.75	0.0539						
						MS	6.06	9.82	0.0203	X					
				1. <i>Papio</i> F(9)	2. <i>Mandrillus</i> F(6)	n-ba	73.33	75.75	0.7057	X					
						n-o	160.33	156.50	0.6671						
						ba-pr	108.67	123.83	0.4156						
						n-pr	78.61	81.75	0.8049						
						MS	11.19	13.04	0.5922						
	<i>iunctim</i>	<i>iunctim</i>	genus	1. <i>Papio</i> (17)	2. <i>Mandrillus</i> (10)	n-ba	67.50	73.15	0.2318						
						n-o	157.53	155.65	0.7496						
						ba-pr	91.35	114.55	0.0793						
						n-pr	65.09	76.15	0.2227						
						MS	8.78	11.75	0.1830						
						<i>PAPIO</i>	F, M	<i>iunctim</i>	sex	1. <i>PAPIO</i> F(12)	2. <i>PAPIO</i> M(15)	n-ba	63.71	74.30	0.0306
n-o												154.37	158.80	0.4672	
ba-pr												81.46	114.73	0.0067	XX
n-pr												55.83	79.87	0.0057	XX
MS												7.31	11.93	0.0099	XX

The remaining taxa were created on the basis of the similarity of the genera studied. So, the *PAPIO* taxon consists of the *Papio* genus with four species and *Mandrillus* with two species, thus making a group consisting of 27 individuals. The *HYLOBATES* taxon consists of the *Hylobates* genus with 5 different species and the *Symphalangus* genus with 1 species and contains 15 individuals. The *PAN* taxon is created from 2 genera: *Pan* and *Troglodytes*, with 1 species each and represents 39 individuals, whereas the *PONGO* and *GORILLA* taxa are monotypic, because each of them contains only 1 species (*Pongo pygmaeus* and *Gorilla gorilla*). They include 9 and 25 individuals, respectively.

Next, the significance of the differences between the given taxa according to each of the direct measurements and Morant and Sergi's index were calculated using the Student T-test.

The taxon for the iunctim age groups served as the reference, both separately for females and males and in the case of combining the sexes into a single group.

Hence, we calculated the differences between the ten following pairs of taxa:

- 1) *PAPIO-HYLOBATES*, 2) *PAPIO-GORILLA*, 3) *PAPIO-PAN*,
- 4) *PAPIO-PONGO*, 5) *PAN-PONGO*, 6) *PAN-HYLOBATES*,
- 7) *PAN-GORILLA*, 8) *PONGO-HYLOBATES*, 9) *PONGO-GORILLA*,
- 10) *GORILLA-HYLOBATES*. As an example, we present our calculations for the first pair (Table 3).

Table 3: Statistical comparison of the *PAPIO* and *HYLOBATES* taxa

Significance: X — (5%), XX — (1%), XXX — (0.1%)
 M — male
 F — female

Taxa compared	Sex	Age group	Factor	Sample1 (Count)	Sample2 (Count)	Measurements	Mean 1	Mean 2	Calculated p-value	Significance
<i>I.PAPIO, HYLOBATES</i>	F, M	iunctim	taxon	<i>PAPIO</i> F(12)	<i>HYLOBATES</i> F (5)	n-ba	63.71	55.50	0.1372	
						n-o	154.38	133.90	0.0226	X
						ba-pr	81.46	62.40	0.0643	
						n-pr	55.83	26.00	0.0001	XXX
						MS	7.32	4.10	0.0094	XX
				<i>PAPIO</i> M(15)	<i>HYLOBATES</i> M(10)	n-ba	74.30	57.65	0.0001	XXX
						n-o	158.80	131.55	0.0001	XXX
						ba-pr	114.73	66.90	0.0001	XXX
						n-pr	79.87	29.55	0.0001	XXX
						MS	11.93	4.96	0.0001	XXX
	iunctim	iunctim	taxon	<i>PAPIO</i> (27)	<i>HYLOBATES</i> (15)	n-ba	65.59	56.93	0.0001	XXX
						n-o	156.83	132.33	0.0001	XXX
						ba-pr	99.94	65.40	0.0001	XXX
						n-pr	69.19	28.37	0.0001	XXX
						MS	9.88	4.67	0.0001	XXX

Age classes were considered in the calculations to estimate the development rate of the skulls studied. The eight age classes 0–7 were grouped into five classes denoted 0–4, due to the small number of cases and their uneven distribution.

The new codes correspond to the old ones as follows: 0 = 0; 1 = 1, 2; 2 = 3; 3 = 4, 5 and 4 = 6, 7. For example, age group “0” differs significantly from group “1” in the case of the n–ba feature for *Papio* ($p=0.025$). This p -value was calculated using Tukey’s model of variation and multiple comparison analysis [28]. The comparison of taxa using the new age codes is given in Table 4.

Table 4: Number of cases of each taxa according to age group

M — male
F — female

Age group	<i>PAPIO</i>		<i>HYLOBATES</i>		<i>PAN</i>		<i>GORILLA</i>		<i>PONGO</i>	
	F	M	F	M	F	M	F	M	F	M
0	2	0	0	0	1	1	1	0	0	0
1	3	6	1	3	8	8	5	4	2	2
2	4	0	1	2	2	0	0	1	0	0
3	2	3	1	0	3	1	1	0	0	0
4	1	6	2	5	8	7	9	4	4	1
SUM 115	12	15	5	10	22	17	16	9	6	3

Calculations are made separately for each feature. Let

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

be the sample from the i -th class and

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

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

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

where q denotes the appropriate quantile of the studentized-range distribution and σ , the 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

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

Unfortunately, it was only possible to analyze the difference between the taxa studied for two age groups: 1 and 4. The three direct measurements which define the upper facial skull triangle were applied in these comparisons to estimate the development rate. These are **n–ba** (5), **ba–pr** (40) and **n–pr** (48). The choice of these measurements appeared to be crucial, for example in the case of the *PAPIO* taxon, when differentiating between age classes from 0 to 7 using all the features analyzed and also for Morant and Sergi’s index (Table 5).

Table 5: Analysis of differences between measurements and the Morant and Sergi’s index in age groups 1 and 4 for the *Mandrillus* and *Papio* genera, as well as for the general *PAPIO* taxon.

Significance: X — (5%), XX — (1%), XXX — (0.1%), NA — not available.
M — male
F — female

Nº	Genus/Taxon	Sex	ba–pr	n–pr	n–o	n–ba	MS
1	<i>Mandrillus</i>	F	NA	NA	NA	NA	NA
2	<i>Mandrillus</i>	M	XX	X	-	XX	-
3	<i>Mandrillus</i>	F+M	XXX	X	-	XX	-
4	<i>Papio</i>	F	-	X	-	XX	-
5	<i>Papio</i>	M	X	-	-	XX	-
6	<i>Papio</i>	F+M	XX	XXX	X	XXX	XX
7	<i>PAPIO</i>	F	-	XX	-	XX	-
8	<i>PAPIO</i>	M	XXX	XX	-	XXX	-
9	<i>PAPIO</i>	F+M	XXX	XXX	-	XXX	-

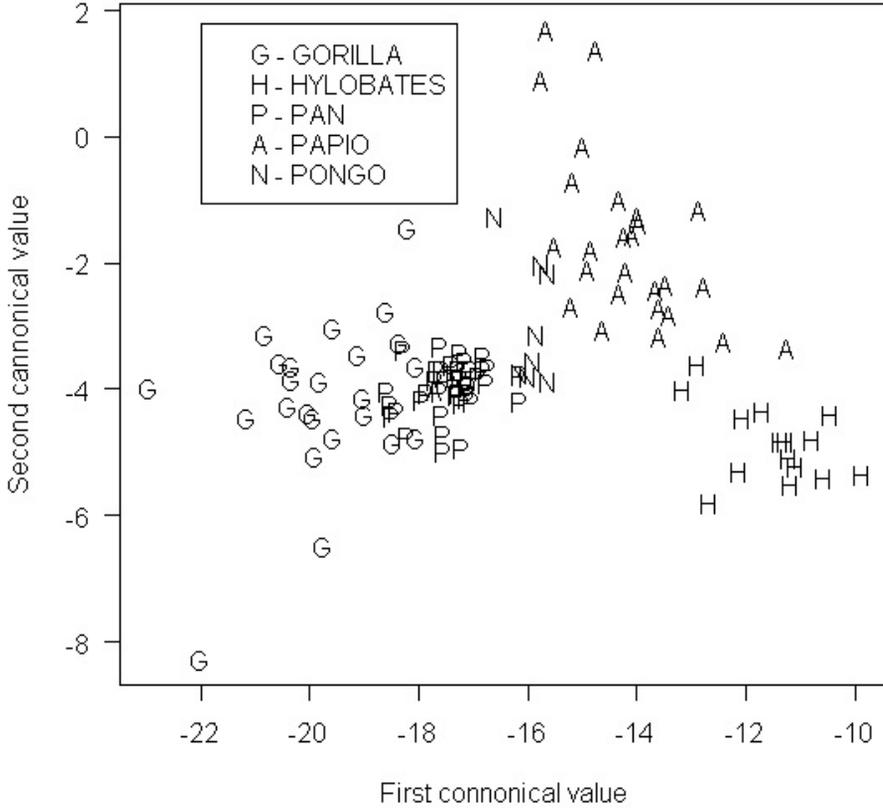
The differences between all the taxa for the features singled out above in those age groups which can be compared, i.e. 1 and 4, are presented in Table 6.

Table 6: The differences between chosen taxa in age groups “1” and “4”
 Significance: X — (5%) , XX — (1%), XXX — (0.1%); iunct-iunctim

Taxa compared	Sex	Age group	Factor	Sample 1 (Count)	Sample 2 (Count)	Measurements	Mean 1	Mean 2	Calculated p -value	Significance
1. <i>PAPIO</i> , <i>PAN</i>	iunct.	1	taxon	9. <i>PAP</i>	16. <i>PAN</i>	n-ba	61.66	74.97	0.0001	XXX
						ba-pr	79.94	89.37	0.0800	
						n-pr	54.33	58.12	0.3419	
2. <i>PAPIO</i> , <i>PONGO</i>	iunct.	1	taxon	9. <i>PAP</i>	4. <i>PON</i>	n-ba	61.66	76.75	0.0001	XXX
						ba-pr	79.94	100.12	0.0053	XX
						n-pr	54.33	59.25	0.2158	
3. <i>PAN</i> , <i>PONGO</i>	iunct.	1	taxon	16. <i>PAN</i>	4. <i>PON</i>	n-ba	74.97	76.75	0.3786	
						ba-pr	89.37	100.12	0.0493	X
						n-pr	58.12	59.25	0.6052	
4. <i>PAN</i> , <i>HYLOBATES</i>	iunct.	4	taxon	15. <i>PAN</i>	7. <i>HYL</i>	n-ba	99.97	64.21	0.0001	XXX
						ba-pr	134.47	77.21	0.0001	XXX
						n-pr	82.60	33.00	0.0001	XXX
15. <i>PAN</i> , <i>GORILLA</i>	iunct.	4	taxon	15. <i>PAN</i>	13. <i>GOR</i>	n-ba	99.97	124.19	0.0002	XX
						ba-pr	134.47	166.31	0.0008	XX
						n-pr	82.60	108.54	0.0001	XXX
6. <i>GORILLA</i> , <i>HYLOBATES</i>	iunct.	4	taxon	13. <i>GOR</i>	7. <i>HYL</i>	n-ba	124.19	64.21	0.0001	XXX
						ba-pr	166.31	77.21	0.0001	XXX
						n-pr	108.54	33.00	0.0001	XXX

All the features discussed constitute a multi-dimensional space in which particular taxa are described. Four direct measurements which constitute Morant and Sergi’s index were used in the study of relations to calculate similarities between the taxa studied.

Figure 2: Results of discriminant analysis based on four direct measurements.



Legend: the first canonical coordinate indicates a multi-dimensional distance as a projection on the horizontal axis, and the other one - on the vertical axis.

Figure 2 shows the projections of points in four dimensional space corresponding to the skulls in the sample into the two dimensional subspace spanned by the first two canonical vectors. By definition, Koronacki, Ćwik [12], the i -th canonical vector is the eigenvector of

$$S^{-1}B$$

corresponding to the i -th largest eigenvalue, where S and B are the within-class and between-class variance-covariance matrices, respectively. If

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

is the sample from the i -th class (in our case — taxon), then:

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

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

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

The Mahalanobis distances [14] between the taxa studied are given in Table 7.

Table 7: Mahalanobis distances between taxa.

TAXON	<i>PAPIO</i>	<i>HYLOBATES</i>	<i>PAN</i>	<i>GORILLA</i>	<i>PONGO</i>
<i>PAPIO</i>	0.00	4.18	3.95	5.91	2.68
<i>HYLOBATES</i>	4.18	0.00	6.01	8.20	5.06
<i>PAN</i>	3.95	6.01	0.00	2.34	1.94
<i>GORILLA</i>	5.91	8.20	2.54	0.00	4.01
<i>PONGO</i>	2.68	5.06	1.94	4.01	0.00

These distances are calculated according to the formula:

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

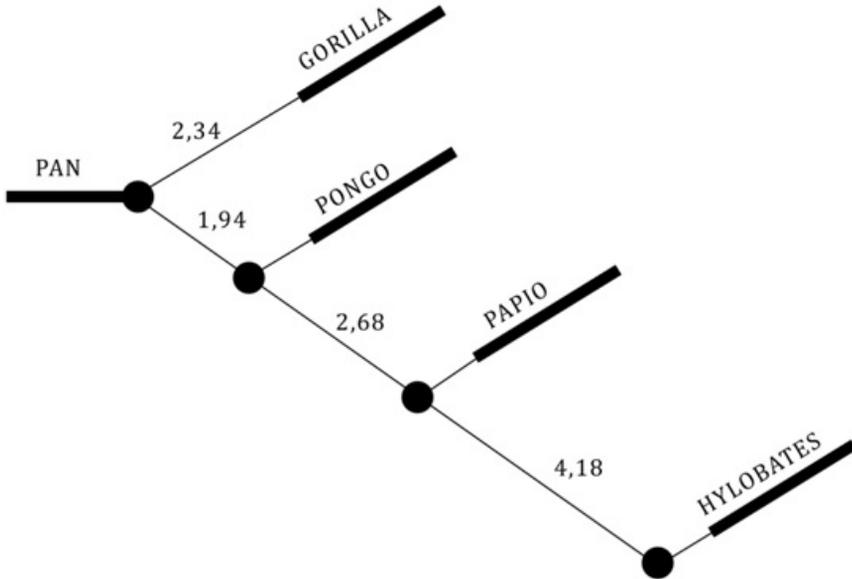
An evolutionary tree based on the Mahalanobis distances between taxa is shown in Figure 3. It is assumed that these Mahalanobis distances characterize the evolutionary distances between the morphologies of the primates studied.

All these statistical calculations were done with the help of the statistical software package R [19] using the methodology of Venables and Ripley [30].

3. Results The analysis covers the following issues: determining taxa which link genera and species, determining significant differences between the chosen taxa, first regardless of age and sex, afterwards taking sex into consideration and discussing the influence of age on the differences observed between the taxa.

3.1. Determining taxa The calculations concerning the creation of the *PAPIO* taxon (Table 2) show that significant differences between the *Papio* and *Mandrillus* genera in the case of females occur for Morant and Sergi's index ($p = 0.0203$) and in the ba-pr measurement ($p = 0.0270$). As for males, there are no significant differences at all. One can suppose that male

Figure 3: Evolutionary tree based on Mahalanobis distances between primate taxa



and female baboons have different skull development paths. When comparing both sexes, significant statistical differences can be observed within the whole *PAPIO* taxon in most of the features studied: ba-pr ($p = 0.0067$), n-pr ($p = 0.0057$), MS ($p = 0.099$). Thus, *PAPIO*'s sex dimorphism exceeds the differences between the *Papio* and *Mandrillus* genera and, therefore, they can be attributed to a common taxon. The calculations concerning the *PAN* taxon show that there are no significant differences between the *Pan* and *Troglodytes* genera in the skull features studied, neither between the sexes within combined age groups.

3.2. Studying taxonomic differences There are significant differences between the taxa except for *PAN* and *PONGO*. The chimpanzee (*PAN*) only has a bigger cranial vault than the orangutan (*PONGO*) according to the n-

o measurement when individuals of both sexes are considered ($p=0.0284$). The *PONGO* and *GORILLA* taxa differ significantly, especially in such cranial measurements as n–ba ($p = 0.004$, $p = 0.0407$, $p < 0.0001$) and n–o ($p < 0.0001$, $p = 0.0039$, $p < 0.0001$) calculated for females, males and all individuals, respectively. In addition, the gorilla has a larger vaulted cranium (higher n–o value). More significant differences between the *PAN* and *GORILLA* taxa are observed in females than males. Apparently, certain taxonomic differences among males are masked by strongly marked male sexual features. However, there is no significant difference between the ratio of neurocranium to viscerocranium size (MS index) in males from the *PAN* and *GORILLA* taxa ($p = 0.2318$). The developmental lines of *PAPIO* and *HYLOBATES* differ greatly in the skull features studied, only the n–ba ($p = 0.1372$) and ba–pr ($p = 0.0643$) measurements among females show no significant difference. The *PAPIO* taxon is much more similar to *Pongidae* than *HYLOBATES*. According to our calculations, *HYLOBATES* constitutes a much different evolutionary path from the other taxa.

3.3. Discussing the influence of age on the differences observed between the taxa

The calculations presented in Table 6 show that in age group 1 young *PAPIO* individuals (aged 1–3 years) and those of the *PAN* and *PONGO* taxa (aged 3–6 years) do not differ much. The measurement which distinguishes the *PAPIO* taxon from the other two is n–ba ($p = 0.0001$), which is based on a chord separating the *viscerocranium* from the *neurocranium*. The *PAN* and *PONGO* taxa are even more similar, only one significant difference in the measurements — ba–pr ($p = 0.0493$). In the group of morphologically mature primates (age code 4), there is a considerable difference between the following pairs of taxa: *PAN-HYLOBATES*, *PAN-GORILLA* and *GORILLA-HYLOBATES*, in all the features ($p < 0.0001$). This proves that these primates have different ancestral lines.

4. Conclusions

On the basis of the calculations concerning the variability of direct measurements and of Morant and Sergi's index, the following conclusions can be drawn:

- *PAN* is the taxon which constitutes the central form in the development of the apes examined. It can be assumed that evolution proceeded from this initial form representing the features of a chimpanzee skull and leading in one direction to the taxon of *PONGO* (orangutan) and in another direction to the *GORILLA* taxon.
- The taxon of *GORILLA* has the largest vault and the biggest neurocranium in direct measurements, which corresponds to the gorilla having the largest brain weight in the group of the primates studied.

- According to the characteristics examined, the *PONGO* taxon links to Old World monkeys through the *PAPIO* taxon. This does not mean that these taxa have a close phylogenetic relationship, but that the evolution of the *PAPIO* form may have run in the direction of the great apes through a number of intermediate forms.
- Gibbons (the taxon of *HYLOBATES*) differ equally from both baboons (*PAPIO*) and the greater apes, but at the same time they are closest to *PONGO*. It can be assumed that they present a special form with their own individual trend in the evolution of skull structure. This is manifested in the smallest values of both direct skull measurements and Morant and Sergi's index among the forms studied, which, as a result, gives the highest relative size of the *neurocranium*. However, it is the absolute weight of a brain that matters in terms of the evolution of primates, which allows the development of certain centres in a primate's brain, as described by Falk [7]. According to Eccles [6], the brain index for *H. sapiens* is equal to 33.79, whereas for great apes — 11.19 and for monkeys — 8.12.
- The analysis of the rate of skull development in the primates studied indicates that young individuals are relatively similar to each other, irrespective of taxonomic differences. The difference between the taxa is only visible in the period of morphological stability.
- The sex dimorphism of baboon and mandrill skulls slightly exceeds the taxonomic differences only among females, which gives evidence for their developmental parallelism to males.
- Our results support the hypothesis of polyphyletism in primates as proposed by Szalay and Rosenberger [26].

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Ewolucyjne etapy sformalizowanych taksonów niektórych małp zwierzokształtnych i człekokształtnych.

Streszczenie. Celem pracy jest przedstawienie sformalizowanych taksonów łączących różne gatunki i rodzaje jako etapy morfologiczne ewolucji naczelnych. Materiał badawczy zawiera 115 czaszek małp zwierzokształtnych i człekokształtnych. Stosunek zmienności ich mózgowczaszki do twarzoczaszki scharakteryzowano wskaźnikiem Moranta i Sergiego [21, 25] oraz pomiarami bezpośrednimi, które go tworzą. Analiza wyników pozwala na poniżej sformułowane wnioski. Przy tworzeniu dla pawianów taksonu *PAPIO* wykazano, że różnice między samcami i samicami są większe niż międzygatunkowe czy międzyrodzajowe. Wskazuje to na możliwość równoległego rozwoju samic i samców wśród niektórych naczelnych. W przypadku szympansów [takson *PAN*] nie wykazano istotnych różnic ani między rodzajami, które go tworzą, ani między płcią męską i żeńską. Badaniem istotności różnic między utworzonymi taksonami stwierdzono, że radiacja adaptatywna małp człekokształtnych rozpoczęła się od formy przodka opowiadającemu współczesnemu szympansowi. Gibony [takson *HYLOBATES*] są w podobnym stopniu oddalone od małp zwierzokształtnych jak i człekokształtnych. Można przypuszczać, że stanowią one osobny trend ewolucyjny w budowie czaszki. W przestrzeni rozpatrywanych cech, takson *PONGO* nawiązuje do małp zwierzokształtnych poprzez takson *PAPIO*. Można przypuszczać, że ewolucja pawianów może przebiec poprzez szereg form pośrednich w kierunku małp człekokształtnych odpowiadających opisanej formie orangutana. Analiza tempa i rytmu rozwojowego czaszki wskazuje, że osobniki młode wszystkich badanych naczelnych są do siebie podobne. Zróżnicowanie taksonomiczne między nimi pojawia się dopiero w okresie pełnej dojrzałości warunkującej stabilizację morfologiczną czaszki.

Słowa kluczowe: Polifiletyczny rozwój naczelnych, sformalizowane taksony naczelnych, proporcje czaszki jako wykładnik ewolucji małp.



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