

ZOFIA SIKORSKA-PIWOWSKA (Warsaw)
TOMASZ ŁUKASZUK (Białystok)

Model to generate phylogenetic missing stages of dinosaurs

Abstract Aim of the paper is to present a mathematical method used to generate the missing stages of the evolution of fossil vertebrates. Considered excavations may be in the form of skeletons or the traces left by autopodium during locomotion of these animals. The research material contains selected dinosaurs, which features of locomotor apparatus were described in terms of chronology and habitat affiliation. They were formalized in the form of a numeric code by Sikorska-Piwowska [29]. The present paper has in view taking into account the adaptation and specialization traits of limbs and also the types of autopodium joints and basipodium specializations. The vector of binary features is assigned to each investigated form of *Tetrapoda*. It was taken the simplified assumption of statistical independence and equipose of investigated features during the building of the model. There are no reasons for distinguishing any of them. The projection of the spatial image of dinosaurs' locomotor apparatus development has the expression in the form of mathematical cladogram. This model verifies some evolution stages like origin of pre-birds lined with hypothetic form related with *Coelophysis*, one of the earliest known dinosaurs from upper *Triassic*. In such a manner *Archeopteryx* was left out from considerations as the ancestor of prebirds.

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Key words and phrases: missing stages in phylogenetic of dinosaurs, parallel lineages in dinosaur phylogeny, mathematical model exposing the origin of birds, prebirds associated with *Coelophysis* not with *Archaeopteryx*..

1. Introduction Aim of the paper is to present a mathematical method used to generate the missing stages of the evolution of fossil vertebrates. Considered fossil remains may be in the form of skeletons or traces left by autopodium during the locomotion. The developed method is an attempt to identify the finding based on its locomotor apparatus.

According to Sikorska-Piwowska [29] the types of adaptation and the types of specialization and also the type of construction autopodium (hand or foot) and specialization basipodium (carpal or tarsal parts) were distinguished for the locomotor apparatus. Type of adaptation means the adaptive characteristics of a given state of the limbs correlated with the characteristics of the whole organism. These traits determine an optimal solution of the limbs locomotion functions in a given habitat, such as human bipedalism is optimal

in the terrestrial habitat. A specialization type means structural-functional differentiations of the limbs formed, inter alia, as a result of a specification of certain locomotion functions. An example of this would be the transition from marching to running in horses ancestors, that is a formation of the hoofed specialization from the plantigrade specialization. The types of autopodium joints and basipodium specialization characterize lineages of development of vertebrates [25]. The basis of the classification of these types is the degree of development of the carpus or tarsus bones and the way in which they are connected with zeugopodium (antibrachium or crural parts of limb), also connections within basipodium or with metapodium (metacarpal or metatarsal parts). Mentioned connections determine the functional type of the joint, while the degree of development of particular bones is dependent on the basipodium specialization. The types were discussed and coded in already cited thesis [29]. All mentioned types are called by us the general traits.

The structure of the locomotive apparatus of vertebrates can be also defined by footprints (fingerprints) left by their fossil remains. The elaboration of autopodium shapes and its position during locomotion serve to determine them. This group of traits is called the principal traits.

All traits of the locomotor apparatus are influenced by the habitat. A given form belongs to a specific environment if its locomotor apparatus is adapted to the optimal locomotion in this habitat. In case of the presence of limbs with lack of locomotion function, such as the human upper limb, or atrophy limbs, such as the whale pelvic limbs, we talk about the absence of a specific habitat for them. Moreover each investigated form was placed in time with the accuracy of one geological period.

The formalization of the whole above-mentioned traits was made in the work [29]. The present paper differs from the previous cited one because now before calculations the traits were coded in the form of binary features. The aim was to eliminate the importance of the values used to encode traits. Moreover additional features concerning general traits like locomotion adaptation and specialization types of autopodium and basipodium joints are included.

The vector of binary features is assigned to each investigated form of *Tetrapoda*. It was assumed a statistical independence and equipoise of investigated features during the building of the model. There are no reasons for distinguishing any of them.

The analysis presented in this paper concerns related genera of extant forms of dinosaurs and their fossil ancestors, described generally by Špinar and Currie [31].

2. Material and methods

2.1. Examined forms The material based on the thesis [29] concerned

locomotor apparatus of the ancestors and descendants forms of dinosaurs described by following authors. These forms are listed below.

1) *Romeriscus* Romer 1956, the representative of *Cotylosauria*, *Captorhinomorpha* suborder [11].

The primitive Thecodontia such as:

2) *Chasmatosaurus* Haughton 1924 - *Proterosuchia* suborder [12, 26, 35],

3) *Euparkeria* Broom 1914 - *Pseudosuchia* suborder [8, 19, 34, 35],

4) *Lagosuchus* Romer 1956 - *Pseudosuchia* suborder [5, 35].

At last the representatives of *Theropoda* (*Saurishia* order) such as *Coelurosauria* infraorder like:

5) *Coelophysis* Cope 1889 - family *Podokesauride* [6, 10, 22, 35],

6) *Struthiomimus* Osborn 1917 - family *Ornithomimidae* [6, 10, 25, 32, 34],

7) *Procompsognathus* Fraas 1914 - family *Procompsognathidae* [6, 21, 32, 33],

8) *Compsognathus* Wagner 1859 - family *Coeluridae* [4, 21, 32],

10) *Ornitholestes* Osborn 1903 - family *Coeluridae* [6, 22, 34],

11) *Archaeopteryx* Osborn 1974 - family *Coeluridae* [1, 19, 20, 35].

Carnosauria infraorder such as *Androdemus* and *Tyrannosaurus* were taken into consideration too:

12) *Androdemus* Leidy 1870 - family *Megalosauridae* [15, 32],

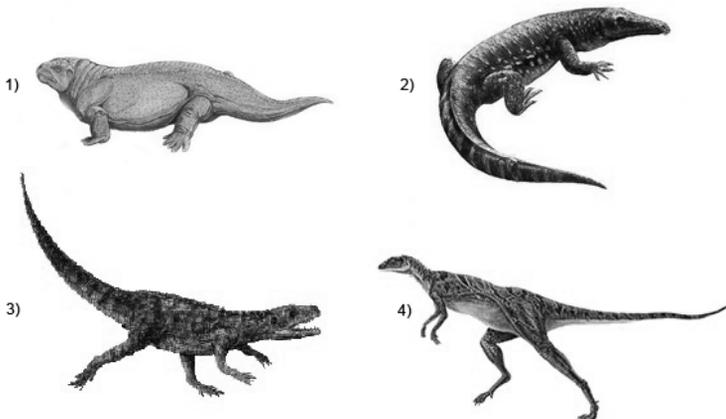
13) *Tyrannosaurus* Osborn 1905 - family *Tyrannosauridae* [25, 32, 33, 35].

Moreover hypothetical a form of *Procarinata* was introduced:

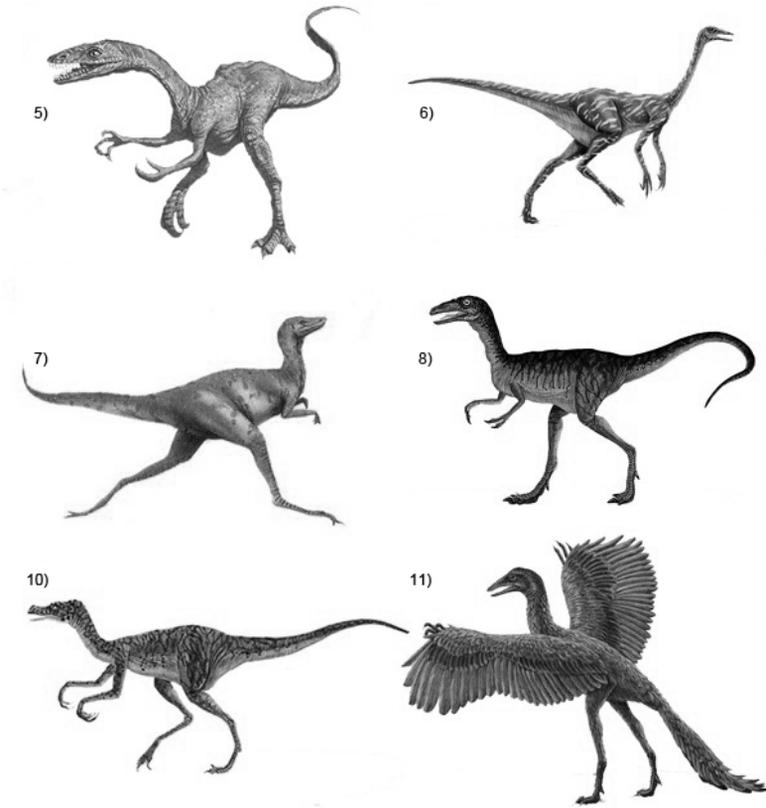
14) *Procarinata* hypothetic form [3, 18, 29].

The figures 1, 2 and 3 illustrate the silhouettes of the above mentioned representatives.

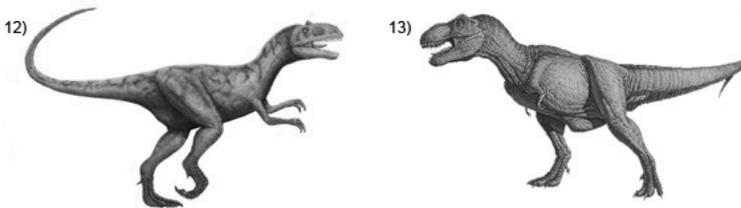
Figure 1: *Romeriscus* and Thecodontia.



Legend: 1) *Romeriscus*, 2) *Chasmatosaurus*, 3) *Euperkeria*, 4) *Lagosuchus*.

Figure 2: Coelurosauria.

Legend: 5) Coelophysis, 6) Struthiomimus, 7) Procompsognathus, 8) Compsognathus, 10) Ornitholestes, 11) Archaeopteryx.

Figure 3: Carnosauria.

Legend: 12) Antrodemus, 13) Tyrannosaurus.

The traits were separately described for pectoral and pelvic limbs, because they can act in different environments and belong to different adaptation and specialization types. E.g. the wing of a bird is adapted to fly

in the aerial (like an eagle) or subaquatic (like a penguin) habitat, but the pelvic limb in a bird can be used for jumping from branch to branch (like a sparrow), walking on the ground (like a pigeon) or swimming (like a duck).

2.2. Habitat types Seven habitat types are distinguished: 1 - bottom, 2 - subaquatic, 3 - epiaquatic, 4 - aerial, 5 - arboreal, 6 - aboveground, 7 - underground. The habitat may have a different effect on pectoral and pelvic limbs of the same form. In connection with it, habitat types are separately considered for both limbs, e.g. the pectoral limbs of a duck are adapted to an aerial habitat, but its pelvic limbs to an epiaquatic habitat.

2.3. Characters of locomotory apparatus The following traits were distinguished separately:

1. General traits referring to the skeleton as dynamic system.
2. Basic traits which can be determined based on an incomplete skeleton or even on a trace left by the hand or foot.

2.4. General traits of locomotory apparatus These traits define:

- adaptation types – code A,
- specialization types – code B,
- autopodium joint types and their functional specialization – code TP.

2.5. Basic traits of extremities These are:

- autopodium shape digital patterns - code RM,
- autopodium position during locomotion – code PA,
- stylopodium position during locomotion – code PS.

Both extremities (pectoral and pelvic) were divided into common segments.

1. Zonopodium consists of shoulder blade or hip bone.
2. Stylopodium concerning brachial or femoral segments.
3. Zeugopodium consists of antebrachium or crural parts.
4. Autopodium referring to hand or foot. There were three parts inside autopodium: basipodium – carpal or tarsal parts, metapodium – metacarpal or metatarsal parts, akropodium - digital parts.

2.6. General traits in examined material Three adaptation types of pectoral extremities were distinguished: quadrupedal (code A1) with two specialization types: semiplantigrade (code B2) and digitigrades (code B3), former quadrupedalism (code A19) with specialization digitigrades (code B3), and flying avian adaptation type (code A15) with one specialization – active flight (code B11).

In the pelvic limb tested forms represent two adaptation types: quadrupedal type (code A1) with semi-plantigrade specialization (code B2) and digitigrades specialization (code B3). Second adaptation is bipedal type featuring archosaurs and birds (code A5) with digitigrade specialization (code B3).

All adaptation and specialization types for vertebrates were described by Sikorska–Piwowska [29].

The quadrupedal type of adaptation is the original adaptation of terrestrial vertebrates. In the semi-plantigrade specialization the autopodium contacts with the ground by his metapodial part. Segments of the limbs (zonopodium, stylopodium, zeugopodium and autopodium) are equal. In the digitigrade type of specialization the fulcrum of autopodium are in the middle phalanges of fingers. The limbs are characterized by elongation of the dorsal elements of zonopodium as shoulder blade and hip bone and elongation of the medial part of zeugopodium in the form of the radius and tibia. The abdominal elements of zonopodium such as clavicle and pubic and ischium bones are shortened. Stylopodium is less developed than zeugopodium. The bones of the fingers compared to the metacarpals and metatarsals are also shortened.

The type of adaptation of the former quadrupedalism refers to pectoral limbs that have lost the support functions. Under the influence of the natural selection these limbs have been adapted, inter alia, to the defense functions.

In case of the pelvic limb we have the quadrupedal type of adaptation (code A1) and the bipedal of archosaurs and birds type of adaptation (code A5). It is characterized by hip acetabulum in varying degrees perforated, femur located parasagittal, gradual reduction of fibula and concrescence of further series of tarsal with bones of metatarsal (midfoot).

The adaptation types were marked by codes A1 to A21, and the specialization types by codes B1 to B13.

The types of autopodium joints and the basipodium specialization were coded on two positions (code TP). In the pectoral limb a basic type of the autopodio-zeugopodial articulation is the antebrachial – carpal joint in all *Tetrapoda*. It is coded with T1. The joint can be differently or similarly shaped and mobile in particular locomotion adaptation and specialization types which are ambivalently identified. For example, immobilization of this joint occurs both in specialized natatory adaptation and in some flight phases in birds. As a basis of specialization of this joint presence and number of central bones of carpus constituting a primitive trait were assumed. Thus, in

case of at least two central bones the specialization is coded P0 as primitive, in case of one bone the specialization is coded P1 as transitory, while the lack of central bones is defined as advanced and coded P2. For instance, the type of autopodium joint and its functional specialization in *Procarinata* are marked with T1P2.

In the pelvic limb autopodium joint types and their functional specializations characterized main phyletic lineages of vertebrates [25]. So there are three main types of foot joints: primary-tarsal-metatarsal, characteristic for amphibians and primitive reptilians, coded T.1, tibial-tarsal characteristic for the lineage of mammals coded T.2 and mesotarsal occurring in advanced reptilians and birds coded T.3. In the type T.1 seven specializations (coded as P.0 to P.6), in the type T.2 four (P.0 to P.3) and in the type T.3 four (P.0, P.1, P.2, P.3), were distinguished [29]. The analysis of possible transformations of adaptation and specialization types and their combined possibilities of pectoral and pelvic limbs were carried out in the cited thesis. The classification of autopodium joint types and basipodium specializations with reference to given locomotory adaptation and specialization types were also carried out.

Based on cited researches it is used the possibility of testing of phylogenetic connections between investigated forms or exclusions of the connections.

2.7. Principal traits of the locomotor apparatus (code RM)

The autopodium shape is determined by the degree of the morphological development of particular rays and by their length sequence.

Traits of autopodial rays were denoted using the digital pattern. To each ray from one to five a couple of values A.B are subordinated. A assumes values from 0 to 2 and corresponds to appropriate degrees of the morphological development of the ray (0 - reduced ray, 1 - partly reduced, 2 - fully developed). B assumes values from 0 to 5 and corresponds to the ray length sequence. Those five couples of values describe each limb in the sequence from the first to the fifth ray. The sequence is called digital pattern code. This code must be biologically admissible, e.g. if A=0 or B=0, A+B=0. Thus each ray of A=0 is in principle of B=0 value, while the ray of A=1 or A=2 corresponds to a B value in the scale from 1 to 5. At lack of some rays, B assumes the value from 0 to 5-k, where k means the number of reduced rays. E.g. if two fingers are reduced they assume value B=0, while the sequence of length of the remaining rays assumes value from 0 to 3. When no rays are reduced to 0, their lengths are described by values from 1 to 5, value 1 being ascribed to the shortest ray and 5 to the longest one. When rays are equal in length their number is denoted by r and the scale is calculated as 5-r+1. E.g. for paraxony (where the third and fourth rays are equal) the scale is 5-2+1=4 (since r=2).

The autopodium position during locomotion or the position showing an adaptation type in non locomotory limbs are considered. In the reduced limb where the autopodium is absent its position is not considered. Four possible positions of autopodium for each limb (0 - autopodium absent, 1 -

pronational position, 2 – transitional position, 3 – supinational position) were distinguished. The ordering numbers of positions constitute the code of positions.

The following stylopodium positions were distinguished: transversal, parasagittal or horizontal and transitional between transversal and parasagittal and transitional between transversal and horizontal. No transitional position occurs between the horizontal and parasagittal position since they are the result of the opposite tendencies derived from the primitive, transversal position. However a secondary return to a more primitive position may occur. This is exemplified by the transversal position of stylopodium in seals originating from mammals with the parasagittal position of stylopodium. In reduced limbs where stylopodium is absent its position is not considered. The stylopodium positions are coded as follows: 0 – stylopodium absent, 1 – parasagittal, 2 – parasagittal-transversal, 3 – transversal, 4 – transversal-horizontal, 5 – horizontal [29].

2.8. Chronology Each investigated form was placed in time with the accuracy of one geological period. The numerical code is presented in Table 1 [30].

Considered geologic time took era from the Paleozoic to the Cenozoic inclusive. The average duration of ages ranging from 10 to 20 million years, with the exception of the Pleistocene epoch, which lasted about three million years. According to de Queiroz and Mayr [7] the necessary minimum to the formation of subspecies of vertebrates is a period of about 30 thousand years, and the development of genetically-formed species takes about 40-50 thousand years. Thus, within each epoch could be created new species. Moreover, during the most recent epochs the rate of evolution is greater due to the intensity of metabolism associated with increasing radiation possibilities of adaptation. For all these reasons, it is assumed that the considered geological epochs are equivalent units of time.

The lists of traits are shown in Tables 2 and 3.

2.9. Description of the used computational methods and procedures On the basis of the possessed material, in particular the data collected in Tables 2 and 3, we will try to construct a dependency tree between investigated forms. The procedure will be based on the principles defined by cladistics [36]. Cladistics is now accepted as the best method available for phylogenetic analysis, for it provides an explicit and testable hypothesis of relationships among organisms. It has been around for almost fifty years, but has really become popular in the past two decades. The principle behind it is that organisms should be classified according to their evolutionary relationships, and that the way to discover these relationships is to analyze apomorphic or recent traits of organisms. Cladistic analyses are generally run on the computer using the principle of parsimony. This basically means

Table 1: Numerical code of geological periods.

Code	Era	Period	Epoch	
1	Paleozoic	Devonian	Lower	
2			Middle	
3			Upper	
4		Carboniferous	Lower	
5			Upper	
6		Permian	Lower	
7			Upper	
8	Permian	Triassic	Lower	
9			Middle	
10			Upper	
11		Jurassic	Lower	
12			Middle	
13			Upper	
14		Cretaceous	Lower	
15			Upper	
16		Cenozoic	Tertiary	Paleocene
17				Eocene
18	Oligocene			
19	Miocene			
20	Pliocene			
21	Quaternary		Pleistocene	
22			Recent	

that the special computer program generates all possible family trees which would fit the data, and you assume that the simplest one is probably correct.

In our calculations we used one of application included in the package PHYLIP [9]. PHYLIP (the PHYLogeny Inference Package) is a package of programs for inferring phylogenies (evolutionary trees). It is available free over the Internet. Methods that are available in the package include parsimony, distance matrix, and likelihood methods, including bootstrapping and consensus trees. Data types that can be handled include molecular sequences, gene frequencies, restriction sites and fragments, distance matrices, and discrete characters. PHYLIP is probably the most widely-distributed phylogeny package.

In our case we found the most suitable the Fitch application. It bases on the Fitch-Margoliash method and estimates phylogenies from distance matrix data under the "additive tree model" according to which the distances are expected to equal the sums of branch lengths between the forms. It uses the Fitch-Margoliash [14] criterion and some related least squares criteria. It does not assume an evolutionary clock.

Table 2: Comparison of the principal and general traits of locomotor apparatus, habitat types and geological periods - pectoral limb.

Significance: No - number of forms (1 - *Romeriscus*, 2 - *Chasmatosaurus*, 3 - *Euparkeria*, 4 - *Lagosuchus*, 5 - *Coelophysis*, 6 - *Struthiomimus*, 7 - *Procompsognathus*, 8 - *Compsognathus*, 10 - *Ornitholestes*, 11 - *Archaeopteryx*, 12 - *Antrodemus*, 13 - *Tyrannosaurus*, 14 - *Procarinata*), RM - degrees of the morphological development of particular rays and their length sequence, PA - Autopodium position, PS - Stylopodium position, M - Habitat, EG - Geological period, A - Adaptation type, B - Specialization type, TP - Type of autopodium joint and basipodium specialization, HT - Hypothetical traits.

No	RM					PA	PS	M							EG		A	B	TP	HT
	I	II	III	IV	V			1	2	3	4	5	6	7	from	to				
1	2.1	2.3	2.4	2.5	2.2	1	3.0	0	0	1	0	0	1	0	4	4	1	2	1.0	0
2	2.1	2.3	2.5	2.4	2.2	1	3.0	0	0	1	0	0	1	0	8	8	1	2	1.0	1
3	2.2	2.4	2.5	2.3	1.1	1	3.0	0	0	0	0	0	1	0	8	8	1	2	1.0	1
4	2.3	2.4	2.5	2.2	1.1	1	3.0	0	0	0	0	0	1	0	9	9	1	3	1.0	1
5	2.2	2.4	2.3	1.1	0.0	1	3.0	0	0	0	0	0	1	0	10	10	1	3	1.2	0
6	2.1	2.3	2.2	0.0	0.0	1	3.0	0	0	0	0	0	1	0	15	16	1	3	1.0	0
7	2.3	2.4	2.5	2.2	1.1	1	3.0	0	0	0	0	0	1	0	10	10	1	3	1.2	1
8	2.2	2.3	1.1	0.0	0.0	1	3.0	0	0	0	0	0	1	0	13	13	1	3	1.2	0
10	2.1	2.3	2.2	0.0	0.0	1	3.0	0	0	0	0	0	1	0	13	13	1	3	1.2	0
11	2.1	2.3	2.2	0.0	0.0	2	3.0	0	0	0	0	0	1	0	13	13	1	3	1.2	0
12	2.2	2.3	2.1	0.0	0.0	1	3.0	0	0	0	0	0	0	0	13	13	19	3	1.2	0
13	2.2	2.3	1.1	0.0	0.0	1	3.0	0	0	0	0	0	0	0	16	16	19	3	1.2	1
14	2.1	2.3	2.2	0.0	0.0	3	3.0	0	0	0	1	0	0	0	14	14	15	11	1.2	1

Table 3: Comparison of the principal and general traits of locomotor apparatus, habitat types and geological periods - pelvic limb.

Significance: for lettering see Table 2.

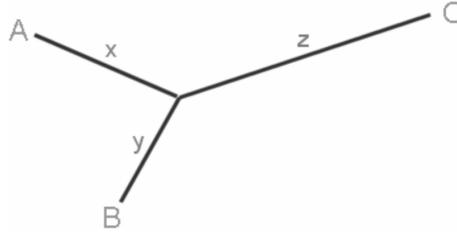
No	RM					PA	PS	M							EG		A	B	TP	HT
	I	II	III	IV	V			1	2	3	4	5	6	7	from	to				
1	2.1	2.3	2.4	2.5	2.2	1	3.0	0	0	1	0	0	1	0	4	4	1	2	1.0	0
2	2.1	2.3	2.4	2.5	2.2	1	3.0	0	0	0	0	0	1	0	8	8	1	2	1.2	0
3	2.2	2.3	2.5	2.4	2.1	1	3.0	0	0	0	0	0	1	0	8	8	1	2	3.0	0
4	2.2	2.3	2.5	2.4	2.1	1	1.0	0	0	0	0	0	1	0	9	9	5	3	3.0	0
5	2.2	2.3	2.5	2.4	2.1	1	1.0	0	0	0	0	0	1	0	10	10	5	3	3.3	0
6	0.0	2.1	2.3	2.2	1.1	1	1.0	0	0	0	0	0	1	0	15	16	5	3	3.3	0
7	2.1	2.2	2.4	2.3	0.0	1	1.0	0	0	0	0	0	1	0	10	10	5	3	3.3	0
8	2.1	2.2	2.4	2.3	0.0	1	1.0	0	0	0	0	0	1	0	13	13	5	3	3.3	0
10	2.1	2.2	2.4	2.3	0.0	1	1.0	0	0	0	0	0	1	0	13	13	5	3	3.3	1
11	2.1	2.2	2.4	2.3	0.0	1	1.0	0	0	0	0	0	1	0	13	13	5	3	3.3	0
12	2.1	2.2	2.4	2.3	0.0	1	1.0	0	0	0	0	0	1	0	13	13	5	3	3.3	0
13	2.1	2.2	2.4	2.3	0.0	1	1.0	0	0	0	0	0	1	0	16	16	5	3	3.3	1
14	2.1	2.2	2.4	2.3	0.0	1	1.0	0	0	0	0	0	1	0	14	14	5	3	1.2	1

The Fitch-Margoliash method as a distance based tree building method rely on a distance measure between investigated forms resulting in a distance matrix. The idea when using distance based tree building methods is that knowledge of the "true evolutionary distances" between forms should

enable us to reconstruct their evolutionary history.

The Fitch-Margoliash method is based on determining the lengths of the edges in the tree shown in Figure 4. Based on the known values of the distance between the nodes D_{AB} , D_{AC} and D_{BC} and the additive property of the used distance metric, the calculating of the distances x , y and z is carried out.

Figure 4: A tree with three nodes, additive property of distance can be used to estimate branch lengths.



Edge lengths x , y , z are given by equations:

$$(1) \quad x + y = D_{AB}$$

$$(2) \quad y + z = D_{BC}$$

$$(3) \quad x + z = D_{AC}$$

Solution is given by the formulas:

$$(4) \quad x = \frac{D_{AB} + D_{AC} - D_{BC}}{2}$$

$$(5) \quad y = \frac{D_{AB} + D_{BC} - D_{AC}}{2}$$

$$(6) \quad z = \frac{D_{AC} + D_{BC} - D_{AB}}{2}$$

The entire Fitch-Margoliash algorithm is implemented in the following steps:

1. In the distance matrix find the closest pair, e.g. A and B.
2. Treat the rest of the forms as a single composite form. Calculate the average distance from A to all of the other forms and B to all of the other forms.
3. Use these values to calculate the distances a and b between A and the joining common node to B and the same for B.
4. Take A and B as a single composite form AB, calculate the average distances between AB and each of the other form, and make a new distance table from these values.

5. Identify the next pair of most closely related forms and proceed as in step 1 to calculate the next set of branch length.
6. When necessary subtract extended branch lengths to calculate lengths of intermediate branches.
7. Repeat the entire procedure starting with all possible pairs of forms A and B, A and C, A and D, etc.
8. Calculate the predicted distances between each pair of forms for each tree to find the tree that best fits the original data.

The above described procedure generates a tree that preserves distances at best. The method is based on the least squares criterion. It tries different tree topologies and recalculated the distances. For each tree considered, a different distances will be generated. The best tree is defined as that one which minimizes the following equation:

$$(7) \quad \sum_{ij} \frac{(D_{ij} - d_{ij})^2}{D_{ij}^2}$$

where D_{ij} is the distance between forms i and j in the input distance matrix and d_{ij} is the predicted distance between forms i and j for particular tree.

In the face of assumption of equal importance of all the traits describing investigated forms, the traits have been converted to the corresponding traits of binary values. It is the necessary condition to bring different features to make them comparable to each other, without distinction of any of them.

The binarization process was as follows. One primary trait was replaced by n of the new traits, where n equals the number of different values, which adopts the primary trait. The values of the new traits are 1 or 0. 1 where the value of the original trait was equal to the value represented by the new trait, and 0 otherwise. For example, the trait describing the type of adaptation of pectoral limb (A1) takes on three different values 1, 19 or 15, therefore, it has been encoded with three new binary traits. The first new binary trait is set to 1 in case of forms that the value of the trait A1 in the Table 2 are set to 1, 0 in the case of other forms. The second new binary trait is set to 1 for the forms that the value of trait A1 equals to 19, 0 in the case of other forms. Similarly, we define the third new binary trait. In this manner we received 118 new traits relating to the two limbs. The calculations do not take into account the primary traits of EG (geological period) and HT (a hypothetical traits). Traits are presented in Tables 4 and 5.

The values of the Euclidean distance between points corresponding to investigated forms are placed into a matrix of distances (see Table 6). Certain distances were not calculated because of the data nature. It results from the biological a priori knowledge pointing certain combinations as illogical.

in “excluded values” places we use the value much greater than all other values of distance, i.e. the value of 1000 (see Figure 5). The Fitch application, of course, treats distance matrix given to its input as symmetrical, so there was a risk that it will generate a tree, which will be unacceptable for us, because it will contain illegal connections. A partial protection was the fact that the Fitch application prefers the order of instances given in the input data file. As a result, we received the tree without illegal connections, so we accepted it.

Table 6: Matrix of distances between investigated forms.

Significance: + - exclusion follows from the comparison of general traits, @ - exclusion follows from the comparison of basic traits and assignment to geological periods, # - exclusion follows from the comparison of no-coded traits.

		descendant												
		1	2	3	4	5	6	7	8	10	11	12	13	14
ancestor	1	@	2,45	4,90	5,66	5,74	5,74	5,92	6,08	5,74	5,92	+	+	6,32
	2	@	@	4,69	5,48	5,92	5,92	5,74	6,08	5,92	6,08	+	+	6,48
	3	@	@	@	3,46	5,00	5,39	4,36	5,39	5,20	5,39	+	+	5,83
	4	@	@	@	@	3,61	4,36	2,65	4,58	4,12	4,36	4,69	4,90	5,10
	5	@	@	@	@	@	+	@	3,46	2,45	2,83	3,61	3,87	3,87
	6	@	@	@	@	@	@	@	@	@	@	@	@	@
	7	@	@	@	@	@	+	@	+	+	+	+	+	+
	8	@	@	@	@	@	@	@	@	@	@	@	1,73	@
	10	@	@	@	@	@	+	@	2,45	@	1,41	2,65	3,00	3,00
	11	@	@	@	@	@	+	@	2,83	#	@	3,00	3,32	3,00
	12	@	@	@	@	@	+	@	+	+	+	@	1,41	+
	13	@	@	@	@	@	@	@	@	@	@	@	@	@
	14	@	@	@	@	@	+	@	@	@	@	@	+	@

Figure 5: The input data for the Fitch application.

```

13
1_Romeri
2_Chasma 2.44949
3_Eupark 4.89898 4.69042
4_Lagosu 5.65685 5.47723 3.4641
5_Coelop 5.74456 5.91608 5 3.60555
10_Ornit 5.74456 5.91608 5.19615 4.12311 2.44949
11_Archa 5.91608 6.08276 5.38516 4.3589 2.82843 1.41421
6_Struth 5.74456 5.91608 5.38516 4.3589 1000 1000 1000
7_Procom 5.91608 5.74456 4.3589 2.64575 1000 1000 1000 1000
8_Compso 6.08276 6.08276 5.38516 4.58258 3.4641 2.44949 2.82843 1000 1000
12_Antro 1000 1000 1000 4.69042 3.60555 2.64575 3 1000 1000 1000
13_Tyran 1000 1000 1000 4.89898 3.87298 3 3.31662 1000 1000 1.73205 1.41421
14_Proca 6.32456 6.48074 5.83095 5.09902 3.87298 3 3 1000 1000 1000 1000 1000

```

2.10. Test possibility of phylogenetic relations The possibility of a direct relationships of a pair of forms from a given phylogenetic lin-

age is tested on the basis of values of three general traits: adaptation types, specialization types, autopodium joint types and their functional specialization. If any of the above tests reveals a reason for an exclusion of a direct relationship of a pair of forms, any further testing will be useless.

Any lack of relationships of any pair of the above traits is marked in the Table 6 by a cross (+).

Based on the biological analysis of transformation possibilities of basic traits, i.e. of digital pattern, as well as autopodium and stylopodium positions some relationships between pairs were excluded. It is marked by @.

Excluded transformations of digital pattern:

- possibility of regrowth of a ray reduced to zero,
- possibility of secondary, full morphological development of a ray.

Excluded transformations of autopodium position:

- change of position of autopodium reduced to zero into pronational intermedial or supinational.

Excluded transformations of stylopodium positions:

- assuming a position by a stylopodium reduced to zero,
- change from position horizontal into parasagittal . This follows from to opposite development tendencies of the stylopodium position in locomotory extremities originating from the most ancestral transversal position.
- change from secondary position into initial position; change from a more specialized position, eg. parasagittal to a less specialized position, eg. primary transversal position.

Rules of time grouping:

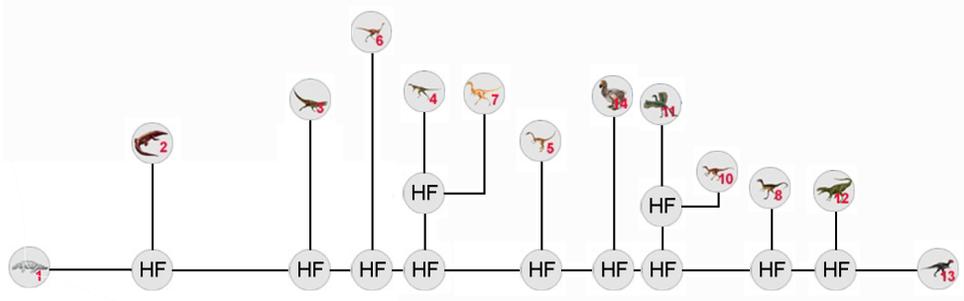
- time grouping is applied one-sidedly, i.e. only an older form or from the same epoch can be ancestor of younger.
- only one time interval is applied as geological duration of a form from the period when the form appeared for the first time to the period until which the form survived.

Using non coded traits is also possible. Thus when estimating possibilities of a direct relationship between a pair of forms in a phylogenetic lineage, other character eg. skulls structures can be compared. Exclusion follows from the comparison of no coded traits. It is in the Table 6 marked by #.

3. Results As a result of Fitch program we received cladogram shown in Figure 6. The cladogram is a graphical presentation of similarities between

the forms. Its vertexes represent particular dinosaur forms. The cladogram points at the evolution stages of investigated forms.

Figure 6: Cladogram of the evolution stages.



Missing evolution links have been pointed by HF. This program calculates the distances basing on binary distance matrix (Table 6). It takes into account not only direct distances between investigated forms but also places between them some hypothetical forms. So the matrix of distances between the binary features in Table 6 concerns the apomorphic traits of investigated reptiles only. To present the cladogram we summarize the edges between hypothetical forms with the edges between these ones and investigated archosaurus.

3.1. Discussion The below formulated conclusions concern original presentation of the archosaur successive evolutionary stages on the basis of formalized traits of their limbs. According to Nesbit and Sterling [17] this subclass of Reptiles is continued today by two extant clades the crocodylians and avians. Our mathematical model is not the faunistical description leading to a modification of these reptiles systematic. The presented method constitutes an universal tool for an objective description of the skeletons and prints of fossil forms. It allows to locate the finds in the space of the vertebrate world in the form of points related to their taxonomy and evolution.

The projection of the spatial image of dinosaurs' locomotor apparatus development has the expression in the form of mathematical cladogram. The cladogram numerous points treat the forms examined. Their apomorphic traits or highly specialised construct the top of phylogenetic branches. Missing evolution stages are considered like hypothetical form.

4. Conclusions

- The cladogram points at the aboveground-epiaquatic form like *Romeriscus* (1), the representative of *Cotylosauria*, as the initial one for the whole phylogenetic lineage of investigated forms. Romer determined it as the oldest reptile living in *Upper Carboniferous* related to primitive *Stegocephalia* [27].

- The thecodont form like *Chasmatosaurus* (2) (also the aboveground-epiaquatic form) has been appointed by the program as one of the oldest forms from the lower *Triassic* and may have been the ancestor of dinosaurs.
- The aboveground thecodont form from lower *Triassic* like *Euparkeria* (3) by hypothetic form led to another stage pointed to *Struthiomimus* (6), the biggest form of *Ornitomimus*. *Struthiomimus* as an ostrich-like dinosaur with a toothless, long neck, long tail, long legs and short arms lived in the late *Cretaceous* period been considered like advanced coelosaur and the fasted dinosaur with hollow bones.
- The same hypothetic form evolving to *Struthiomimus* enlarged to another missing stage pointed to *Lagosuchus* (4) - the thecodont from the middle *Triassic*. Its long hind legs and well balanced body made it a very good hunter, the best of all thecodonts. According to Palmer it was likely an agile predator that could use speed to chase its pray and to escape larger predator [23]. It had bipedal posture. In this evolution way a primitive coelosaur *Procompsognathus* (7) diverged representing suborder *Theropoda*. It may have been one meter long with long hind legs and short arms.
- Ancestral node to *Lagosuchus* led to another hypothetic form pointed at *Coelophysis* (5) one of the earliest known dinosaurs from upper *Triassic* following next hypothetic form to *Procarinata* (14). The last like *Sinosauropteryx* - primitive bird lived in upper *Cretaceous*. This form presented an important stages in theropod evolution [13,28].
- Origin of *Archeopteryx* (11) from the *Jurassic* passed by an ancestral form of *Onitholestes* (10) with hollow bones and strong clawed hand, living in the same epoch. Its hind limbs resembled avian feet. *Archaeopteryx* was a versatile high-end hang gilder in sailplane configuration with exceptional climbing ability. The wing function of *Archaeopteryx* may represent a transition from a cursorial lifestyle to that of a modern flying bird. According to Mike [16] the remains of *Archaeopteryx* could be compared to the remains of feathered, cursorial *Anchiornis* (*A.huxleyi*). Taking all this into account *Archaeopteryx* should not be considered as an ancestor of prebirds.
- Ancestral form of *Jurassic Comsognathus* (8), small, bipedal, carnivour theropod points at the evolutionary parallelism to the representative forms the carnivours *Antrodemus* (12) that refers to *Allosarus* big dinosaur theropod [24]. It seems that *Tyrannosaurus* (13) is nearer to smaller dinosaurs like *Comsognathus* (8) than to greater ones like *Antrodemus* (12). According to Benson [2] *Antrodemus* absent from

Cretaceous was replaced by *Tyrannosaurus* (13), that is confirmed by our cladogram. Moreover *Megaraptor* (*Neovenatoridae*) that lived in this period too, presented *Coeulosaur* traits.

- The created model can be used to test the relationship between investigated forms, verify hypotheses concerning missing stages of evolution, reconstruct initial forms and identify missing evolution links. In comparison with the base thesis [29] the differences between the phylogenetic links of dinosaurs result from the use of general traits of the locomotor apparatus in calculations and from the introduction of the binary values. The above model could be used to elaborate the evolutionary stages of all *Tetrapoda* if their fossil remains allow to define the traits used in this model.
- In the area of the examined characteristics, archosaur taxons refer to *Tetrapoda* evolution. This does not mean that these taxons have closed phylogenetic relationship between them but that the evolution of them passed through a number of intermediate forms that might run in the direction of taxons, up to avian forms.

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Model generujący brakujące ogniwa ewolucji dinozaurów

Streszczenie Celem pracy jest przedstawienie matematycznej metody służącej do wygenerowania brakujących etapów ewolucji kopalnych kręgowców. Rozważane wykopalka mogą występować w postaci szkieletów lub odcisków naskalnych. Materiałem badawczym są wybrane dinozaury, których cechy aparatu lokomocyjnego zostały opisane w kategoriach czasu i przynależności do danego środowiska oraz sformalizowane przez Sikorską-Piwowską [29]. Obecna praca ma na celu włączenie do obliczeń cech adaptacji i specjalizacji kończyn oraz typów stawów autopodium (rąk i stóp) i specjalizacji basipodium dotyczącego nadgarstka i stępu. Konstruowany jest model mający zastosowanie do testowania połączeń między badanymi formami i wyznaczenia brakujących etapów ewolucji. Każda badana forma została oznaczona wektorem binarnym cech. Do budowy modelu przyjęto uproszczone założenie statystycznej niezależności i równoważności badanych cech, ponieważ nie ma podstaw do wyróżnienia którejkolwiek z nich. Projekcja form rozwojowych aparatu lokomocyjnego dinozaurów, jako punktów w wielowymiarowej przestrzeni cech, została wyrażona matematycznym kladogramem. Model ten weryfikuje między innymi stadia rozwojowe ptaków wiążąc je z *Coelophysis* - jedną z najwcześniejszych form dinozaurów pochodzących z górnego Triasu. *Archaeopteryx* zwany mylnie praptakiem został wykluczony z linii prowadzącej do ptaków.

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Słowa kluczowe: brakujące ogniwa w filogenezie dinozaurów, paralelizm rozwojowy dinozaurów, matematyczny model pochodzenia ptaków, pierwotne ptaki powiązane z *Coelophysis* a nie z *Archaeopteryx*..



Zofia Sikorska-Piwowska was born in Warsaw (Poland). She received Ph. D. degree in natural science (1966) and post doctoral title (1984) from University of Warsaw, Department of Biology. From 1990 she was professor at Medical University of Warsaw, Faculty of Medicine and from 1995 at University of Podlasie in Siedlce, Faculty of Agriculture, Institute of Biology. She retired in 2003 and from that time she co-worked with mathematicians in the field of anthropogenesis on topics like: evolution or creationism, hominization tendencies in the evolution of primates in multidimensional modelling, developmental parallelism in primates, evolution of human speech and so on. From 1971 to 1976 she cooperated with Algerian government as associated professor at University of Oran. Since 1978 she has been an active member of Exploration Society of Warsaw visiting and researching in many countries in South Asia like: India, Malaysia, Thailand, China, Japan, in South America like: Venezuela, Ecuador, Galapagos Islands, Guyana, Chile and Brasil, in Africa like: Kenya, Tanzania, Ethiopia and so on.



Tomasz Łukaszuk was born in Białystok (Poland). He received Ph. D. degree in computer science from Białystok University of Technology in 2011. He is the specialist in the field of software engineering and web applications. His research interests are focused on data mining, in particular, feature selection and classification. He has programming experience covering both research projects and commercial solutions.

ZOFIA SIKORSKA-PIWOWSKA
 MEDICAL UNIVERSITY OF WARSAW
 DEPARTMENT OF DESCRIPTIVE AND CLINICAL ANATOMY, CENTER OF BIOSTRUCTURE RESEARCH
 UL. CHAŁUBIŃSKIEGO 5, 02-004 WARSZAWA, POLAND
 E-mail: zofiasikorska@poczta.onet.pl

TOMASZ ŁUKASZUK
 BIAŁYSTOK UNIVERSITY OF TECHNOLOGY
 FACULTY OF COMPUTER SCIENCE, UL. WIEJSKA 45A
 15-351 BIAŁYSTOK, POLAND
 E-mail: t.lukaszuk@pb.edu.pl

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