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Development of human limbs

Abstract

This work offers a new view on the developmental history of tetrapods. It proposes an original evolution model of human limbs based on metameric formation of osteogenic buds in accordance to primary segmentation and biplanar symmetry. While going through evolution, osteogenic buds initially identical to each other were changing their sizes, realigning, regressing, uniting while keeping the direction of the formation in accordance to the following formula (taking into account sesamoid bones): 2; 1; 2; 3; 2; 3; 5; 5; 8; 8 (in the upper limb together with the upper limb girdle); 3; 2; 3; 2; 1; 2; 8; 8; 5; 5 (in the lower limb together with the pelvic bones).

Key words: tetrapods, limb development, symmetry, segmentation.

Introduction

Discovery of laws governing the evolution of the human body structure is one of the most important tasks of biology. However, there are different views on the mechanisms of the human limb development. Scientists generally accept that human limbs developed from fish fins but it is not clear what type of fins could give origin to the five-finger limb. There are two major views on this point. Some hold that the limbs of terrestrial vertebrates developed from fish fins with a single ray in the inner skeleton while others believe they developed from common fish fins having a limited number of such rays [15].

We propose an original concept of the human limb development. This concept is based on the hypothesis that biological objects have a biocrystalloid structure that imparts symmetry and determines segmentation of live organisms [25, 27]. Therefore its brief explanation with references to certain stages in the evolution of early human ancestors should precede the presentation of the concept as such.

Theoretical assumptions

The human organism is a biocrystalloid in a sense that it is regarded both at the level of the whole organism and individual cells as a composite entity consisting of a crystal-like structure and pericrystalline medium. Crystallographic analysis of biological and non-biological minerals does not reveal any significant differences between the two, which is indicative of common crystallization processes [1, 4, 17, 18]. The main feature of crystal structures is their symmetry. Two-plane symmetry is characteristic of man, which is determined by two-plane symmetry of a chromosome, which is carrying genetic information. Aggregation is one of the fundamental features of minerals as they are found not only as separate objects but also as aggregates, i.e. regular cohesive individuals and other synmineralogical systems. This feature is inherent not only to compound molecules but also to associates of a higher order. The cell biology [13] has shown that when similar cells touch each other

they tend to cohere forming aggregates characteristic of the given cell population. Ability to aggregate in an orderly way is expressed as self-organization. Self-organization of live matter and tissue formation depend to a great extent on inter-cellular assembly mechanism, which involves both simple and macromolecules. The integration of cells is controlled by molecular mediators and involves intermolecular interactions [10].

Similar live systems and their components that perform the same function have an ability to integrate and form firstly a conglomerate (colony) and then an organism. This could happen in the development of separate cells into an organism like volvox, a ball-like organism that initially was a colony and then transformed into a single organism. This phenomenon is characteristic of multicellular organisms as well. Integration explains association of multicellular entities into a single multi-segment organism. Later similar organisms consisting of different number of segments also integrated, i.e. the resulting organism consisted of two different but of the same type specimens, each of which had different number of segments. Segmentation is nothing else but traces of integration of separate multicellular non-segmented entities into a whole organism accompanied by gradual fading of differences between them and formation of a single organism in compliance with formation laws. In this integration process the number of symmetry planes could change and not all organisms would build their antimeres in the same way when going from a three-plane to a two-plane symmetry. Some animals arranged antimeres into a row observing the metamerism law and the resulting metameric row became longer (this group includes the chordates, for example) while others integrated antimeres observing their primary segmentation (this group includes the arthropoda).

We can postulate a hypothesis that animal segmentation is a result of aggregation of simple non-segmented biocrystalloid organisms initially into a colony and then into a single segmented organism with gradual fading of the original aggregation traces [26, 27].

Phylogenetically, an early precursor of man evolved from a simple cell into an integrated multi-segment organism through several stages - initially a simple cell, then a cell colony, later a multicellular non-segmented organism of the volvox type, then an organism like a concave ball similar to Haeckel's gastrea or Mechnikov's parenchymella, then a colony of non-segmented multicellular organisms and finally a multi-segment multicellular organism. Perhaps, colonies consisting of a limited number of organisms turned out to be the most stable ones, which led to the formation of organisms consisting of 2-9 segments. Five-segment organisms were predominant. Later on, whole groups of specimens showed ability to integration. Starobogatov [14] noted that the arthropods consist of two groups of segments: the head group invariably contains 5 segments while the caudal one can contain from 2 to 9 segments. The 13-segment precursor organism of man evolved as a result of integration of 5- and 8-segment organisms.

Modern biology and anatomy do not give a clear description of animal segmentation and of its causes. Scientists consider the humans to be partly segmented. There is no clear idea of the number of

segments in humans. Scientists disagree on the number of somites in man and count from 37 to 44 of them [2]. P. Ivanov [7] provides a comparative analysis of metamerism in animal embryonic development. However he gives no explanation to metamerism as such. He draws a conclusion that the chordates could develop from oligomeric forms, but he gives no explanation as to what made oligomeric forms transform into polymeric ones. Scientists have not solved the question of the origin of terrestrial vertebrates. Besides, there is a disagreement about their mono or polyphyletic origin. Some scientists believe these animals are of polyphyletic origin [19, 20, 21, 28, 29], while others [16, 30] are sure they are of monophyletic origin. Meanwhile, some facts are paid more attention to than others and important arguments of the opponents are undervalued.

Development and segmentation of human limbs

Unpaired fins arose as metameric rows of cartilaginous rods in a continuous fold. Division of the fold resulted in separate plates. Paired fins also arose from metameric rows of cartilaginous rods in the paired originally continuous lateral folds. The metameric structure of myogenic and osteogenic buds suggests metameric construction of these continuous fins in strict conformity with body segmentation [15]. Fore and hind (pectoral and caudal) fins formed as a result of bud rearrangement, development of end pieces of the folds, and reduction of the intermediate region.

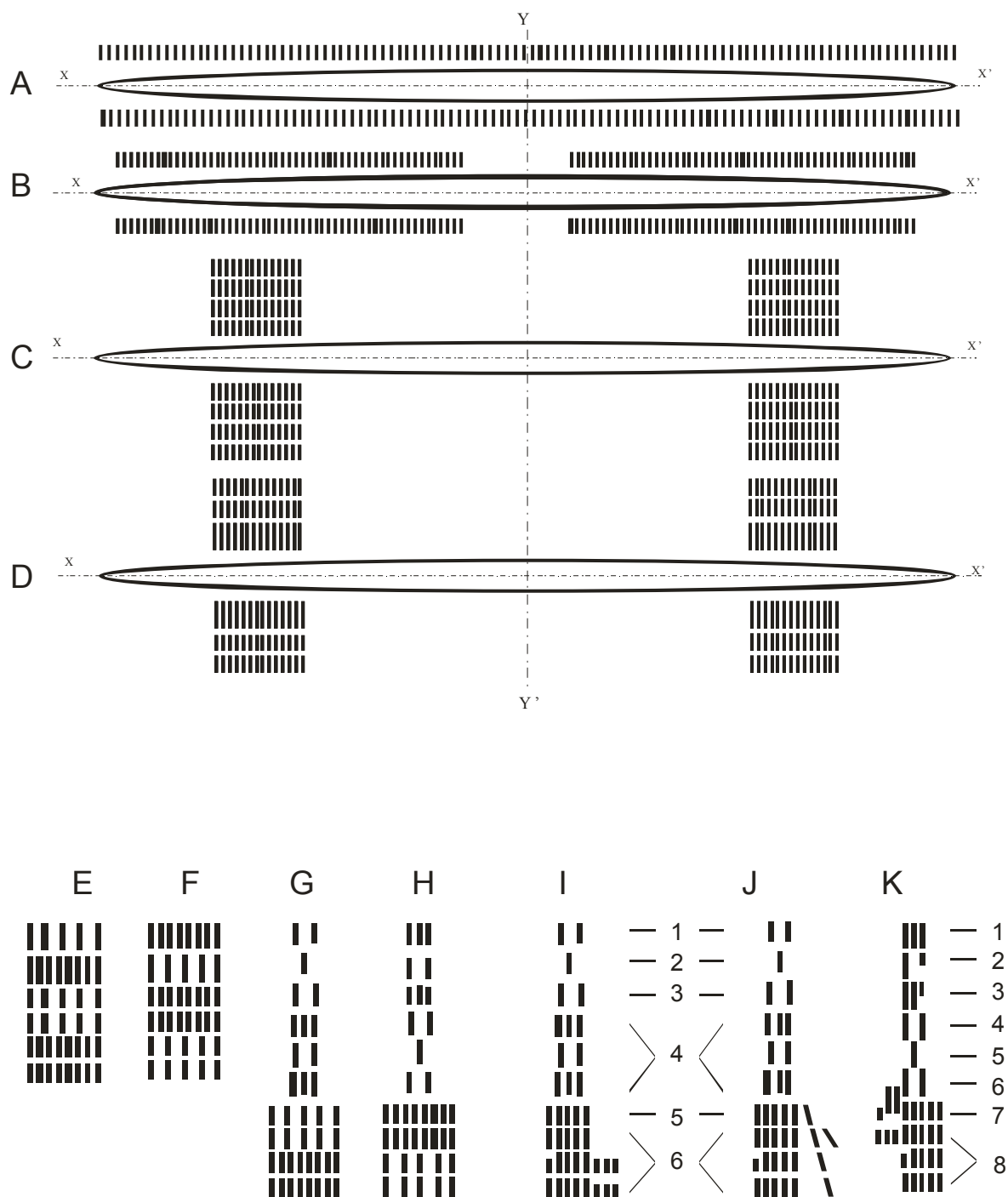


Fig. 1 Scheme of the human limb development.

$x - x'$; $y - y'$ - planes of symmetry.

A - paired continuous lateral fold.

B - D - gradual formation of antimeres with bone anlagen in the two-plane symmetry that served as material for the development of extremities.

B - formation of antimeres with anlagen located in a row.

C - rearrangement of anlagen.

D - partial integration of anlagen in the antimere.

E - K - stages in the formation of extremities with their girdles.

E, G, I, J - formation of the superior extremity; J - 7-ray motion organ.

I, J: 1 - bones of the shoulder girdle; 2 - shoulder; 3 - forearm; 4 - wrist; 5 - metacarpus; 6 - digital phalanges.

F, H, K - formation of inferior extremity.

K: 1 - pelvic bones (ossa ilium, pubis, ischii); 2 - femoral bone (os femoris), sesamoid acetabular bone (os acetabulum); 3 - tibial bones (os tibia et os fibula) and sesamoid patella (os patella); 4 - astragalus (os talus) and heel bone (os calcaneus); 5 - scaphoid bone (os naviculare); 6 - medial and intermediate sphenoid bones (ossa cuneiforma mediale et intermedium); 7 - out of the row are laterosphenoid (os cuneiforma laterale) and cuboid (os cuboideum) bones; in the row are metatarsal bones; 8 - toe phalanges (phalangeal bones).

I, J, K - reduced and sesamoid bones are shown in shorter dashes.

The continuous lateral fold gave rise to 4 groups of bones in agreement with biplanar symmetry and 13-segment division. Each group had 52 buds that later provided material for the formation of paired fins and, finally, extremities. Reduction of the number of limb buds from 52 to 39 appears to have been due to integration and degradation of antimeric elements. Osteogenic buds of each group gave rise to two segments (proximal and distal). The former was made of a single row (13 buds), comprising two groups (5 and 8 buds), the latter consisted of two two-group rows with 13 buds in each (figure 1). Subsequent transformation resulted in an elongated motion organ, containing 6 rows (two in the proximal segment and 4 in the distal one) set up as 5; 8; 5; 5; 8; 8 (for the forelimbs, or upper limbs) and 8; 5; 8; 8; 5; 5 (for hindlimbs, or lower limbs). Along with a rise in the number of rows, bones, formed from the initially equisignificant buds, grew to different sizes. Further complication led to the arrangement of bones in the proximal segment in a six-component sequence whereas the distal segment retained its four rows. Bones in the proximal segment of upper and lower limbs (forelimbs and hindlimbs) were set up according to the scheme 2; 1; 2; 3; 2; 3 and 3; 2; 3; 2; 1; 2 respectively.

It is known that bones reduction in the limbs during the evolutionary process is characteristic of some mammals. It is also characteristic of man. Part of limb bones either transformed into sesamoid bones or reduced completely under effect of morphogenetic factors. The maximum number of sesamoid bones is 28, that is seven in each limb including acetabular bone (os acetabulum) and patella (os patella) and taking into account the non-developed phalanges of the pollicis. In our scheme (figure 1) non-developed and sesamoid bones are shown in short dashes. Sometimes, sesamoid bones of the hand – marked by the letter I, item 6, in our scheme – do not reduce and can realign – they are shown in diagonal dashes under the letter J, item 6. And so bones of the hand form some sort of a seven-rayed fan. Still, the total number of the bones, including the sesamoid ones, never exceeded the number of primary buds corresponding to that of primary segments in organisms with biplanar symmetry.

Construction of the human upper extremity (together with the shoulder girdle) almost ideally comes within the above scheme – 2, 1, 2, 3, 2, 3, 5, 5, 8, 8 (see figure 1, letter J). Osteogenic buds in the proximal segment of the evolving upper extremity of man gave rise to 13 bones, viz. shoulder blade (os scapula), clavicle (os clavícula), humeral (os humerus), radial (os radius), and ulnar (os ulna) bones as well as all 8 carpal bones (ossa carpi). Distal buds on the hand developed into metacarpal bones (ossa metacarpi) and phalanges. It is worth noting that anatomical position of carpal bones does not permit to reliably determine the exact number of their rows although certain anatomists distinguish two rows, the proximal one and the distal one [11, p. 62]. However, we can suppose that their arrangement corresponds to the pattern: 3, 2, 3. The three bones - navicular bone (scaphoideum), lunate bone (os lunatum) and triquetral bone (os triquetrum) – make the first row. The three others – trapezoid bone (trapezoideum), capitate bone (os capitatum) and hamate bone (os hamatum) – make the second row. There are two bones in between them on the sides - trapezium (os trapezium) and pisiform (os pisiforme) bones. Based on the above we can conclude that the sequence of the bones in the upper

extremity of man is the following: two bones of the shoulder girdle, one bone of the shoulder (humeral bone) and two bones of the forearm, then there are bones of the wrist in three rows according to the pattern 3, 2, 3, next there are two rows of five bones each (metacarpal bones (*ossa metacarpi*) make the proximal row, and the first row of the phalanges is the distal row); and the limb ends in two rows of eight bones each including three bones in one row and four in the other that did not develop.

Results of structural studies of human extremities suggest alternation of groups comprising 5 and 8 osteogenic buds each. An upper extremity consists of 5 proximally positioned bones (shoulder blade, clavicle, humeral, radial, and ulnar bones), followed by a group of 8 buds (carpal bones), and two more rows with 5 osteogenic buds in each (metacarpal bones and a proximal row of phalangeal bones). The upper extremities end in two rows of 8 osteogenic buds.

There is every reason to believe that the real structure of the human low extremity (including the pelvic girdle) corresponds to the given scheme: 3, 2, 3, 2, 1, 2, 8, 8, 5, 5 (figure 1, letter K). Osteogenic buds in the proximal segment of the evolving lower extremity gave rise to the following 13 bones: iliac (*os ilium*), pubic (*os pubis*), ischial (*os ischii*); femoral (*os femoris*) and acetabular (*os acetabulum*) bones; calf bone (*os fibia*) and tibia (*os tibia*), patella (*os patella*); and also five of the seven tarsal bones (*ossa tarsi*) including astragalus (*os talus*), heel bone (*os calcaneus*), scaphoid bone (*os naviculare*), medial and intermediate sphenoid bones (*ossa cuneiforma mediale et intermedium*). Distal buds on the leg gave rise to two tarsal bones (*ossa tarsi*), i.e. laterosphenoid (*os cuneiforma laterale*) and cuboid (*os cuboideum*) bones, as well as metatarsal (*ossa metatarsi*) and phalangeal (phalanges) bones.

Thus, the sequence of bones in the lower limb is the following: three pelvic bones, two thighbones (femoral bones), three bones of the crus. Tarsal bones (*ossa tarsi*) are located in accordance to the pattern: 2, 1, 2 – astragalus (*os talus*) and heel bone (*os calcaneus*); scaphoid (*os naviculare*); medial and intermediate sphenoid bones (*ossa cuneiforma mediale and intemedium*). Then there are two rows of eight osteogenic buds each. The proximal row comprises two tarsal bones (*ossa tarsi*) and metatarsal bones (*ossa metatarsi*). One of the bones regressed in this row. As for the distal row, out of the eight buds, three bones did not develop. The lower limb ends in two rows of five bones each and one bone in the toe did not develop.

The sequence of groups consisting of five and eight osteogenic buds described above for the upper extremity is typical of the human lower extremity. The order of sequence is somewhat different, however. The lower limb proximally comprises a group of eight osteogenic buds unlike the upper limb where bones of a five-segment organism are included proximally; these are pelvic bones, thigh bones, tibial bones and patella. In the distal part there are five out of the seven buds of the tarsal bones. And finally, there are two rows of eight osteogenic buds each and two rows of five buds each.

Discussion

One of the most discussed and confusing subjects in biology of vertebrates is the origin of tetrapods. A lot of different fish species had tetrapod-like features in different compositions [6]. In biology this phenomenon is called pre-adaptation. The natural phenomenon was given a wrong name based on the wrong understanding of its essence. The name supposes the fish knew their distant descendants were to leave the water and were getting ready to this event in advance. Found fossils are being thoroughly examined and the results of the examination and analysis are used to create various theories how fins transformed into limbs. Scientists cannot reach an agreement building the rows of transitional forms from the fins of crossopterygian fishes to the single variant of tetrapods' limbs structure. There are hot disputes between scientists when they discuss the consecutive row of different forms of fins of crossopterygian fishes transforming into the pentadactyl limb of the amphibia. After the fossils of tiktaalik were found, a monophyletic line of the fin transforming into the limb was created. We can comment on one of such patterns offered by Daeschler E.B et al. [24]. The pattern shows a consecutive row of transitional mined forms: Glyptolepis, Sauripterus, Eusthenopteron, Panderichthys, Tiktaalik, Acanthostega, and Tulerpeton. The Acanthodes is considered to be the initial form. In our opinion there is no evidence to compile such a row. The fin of the Acanthodes has very few bones to conclude it was the initial form of the multi-element limb of the Amphibia. The fin of Glyptolepis has one ray with over 15 consecutive rows. It is known that the limb of the Amphibia and superior taxons has a multi-ray structure with the number of consecutive rows less than ten. Since the fins of the crossopterygian fishes were only elongating in the evolutionary process, the fin of Glyptolepis cannot be used as the model of limb formation of terrestrial animals. Eusthenopteron, Panderichthys, Tiktaalik had gone a long developmental way by the time they became the fossils and a lot of bone elements had reduced. Authors of hypotheses show in patterns and drawings based on the fossils which bone of the fin transformed into shoulder, radial bone or ulnar bone, the same applies to the hind limb or femoral bone, calf bone and tibia accordingly. When it comes to the carpal and metacarpal bones or the foot, things are completely confused. The subject matter of numerous scientific publications on the stages of fish fin transforming into the tetrapod limb is only about reduction of the number of the fin rays from 10 - 15, according to different authors, in Sauripterus to five in the Amphibia, and description of guesses on how fingers originated in tetrapods. The simplest explanation is that fingers are an acquired innovation [5, 35]. R. Carol [8] says, "...one must suppose that the metacarpals and phalanges of tetrapods developed as almost, if not entirely, new structures".

The major problem in lining up the transitional forms is that the fossil record is far from being complete and it is impossible to unambiguously establish whether one paleobiospecies is the definite ancestor to the other. It is difficult to define when exactly these forms originated. Nobody knows how much time their anagenesis took and it is not clear if their progressive development had reached completion by the time they died. The described above schemes do not correspond to the available data.

Advanced Sarcopterigii lived at the same period as Ichthyostega and Acanthostega. The strongest argument against the offered schemes is the data of the Polish and Swedish scientists who found some traces of a quadruped animal which lived 15 million years earlier than the suppositional first tetrapods [31]. Thus, the harmonious connection between stratigraphy and phylogeny, which stated that transitional fish appeared before tetrapods, was destroyed.

In our opinion the major mistake made by researchers of tetrapodmorphics and tetrapods is their committal to monophyletism. Unwearying efforts to line up all the fossils of the tetrapodmorphics in a cohesive way are not successful. While discussing the origin of the tetrapods, they discuss the reasons causing the fins to transfer into limbs which helped the tetrapods become terrestrials. Biologists share a strong belief that an organ develops when a species needs to adjust to the environment. Leading scientists suggested that fish developed limbs to be able to walk in the shallows [33]. In fact scientists do not give any sound arguments or mechanisms to explain this phenomenon. Their explanations contain a formula “In order to...” and then there are some inventions made by the scientists. These speculations include: in order to find food, keep away from predators, survive the drying up of the reservoirs, etc. At the time when the supposed first amphibians started living on firm-land, these researchers say, there were only plants and insects there. The teeth of the amphibians considered to be the first terrestrials were not fit for chewing insects and plants. Those animals were predators. It is possible to assume that absolutely different chordates were the first to get out of the water and they could serve as food for raptorial tetrapods such as Ichthyostega and Acanthostega. When the reservoirs began to dry up fishes living in the shallows had an opportunity to use suitable for their living environment. Those who did not find it died out. Limbs do not grow because of the drought. Organs are not made by the nature because of some need, to perform some functions or by exercising. The nature does not have an objective. If something is made based on the necessity or intention, it is made by the will of a creator.

We think that it is not possible to solve this problem without renouncing the dominating paradigm of the biology, that is Darwinism, with its monophyletic and divergent formation of species because of natural selection. There are no mechanisms to transfer the newly acquired characteristics of somatic cells to the chromosomes of the germ cells. Acquired characteristics are not inherited via natural selection. Thus, natural selection does not impact the structural organization of the organism. There are no noteworthy ideas on this subject but general speculations on polymorphism and connection of the phenotype with the genotype. In this work, we do not challenge ourselves to entirely cover the problems of evolution. We offer a new view only on the developmental history of tetrapods. Our aim is to describe our own hypothesis of how human limbs developed based on general segmentation and symmetry [27]. Our concept contains several statements:

- 1) All significant changes in the body structure occur due to regular consecutive changes of the germ cells chromosomes elongating from generation to generation in developing species. Structural

reorganization can be the result of both slow accumulation of changes and aromorphosis caused not by random mutations but rather by redistribution and sequestration of genetic material in all the representatives of the species within a short period of time that leads to significant changes of the organism by losing or increasing the existing morphological structures. Due to the sequestration of the genetic material some organs can reduce partly or completely in the new organism. The extreme transformation can consist in formation of new individuals much smaller than their ancestors. Structural changes lead to acquiring new characteristics by viable organisms. Further, the **natural choosing of the environment** meeting the new characteristics of the organism takes place.

2) There is an idea of parallel evolution of closely related groups of animals [9, 32, 34]. Allied species acquire the same set of characteristics and mutation parallelism occurs so constantly that it is possible to suppose there are other non-discovered related species with the same set of characteristics. This is the essence of the law of homologous series disclosed by N. Vavilov [3]. The parallel development law explains the same set of characteristics in different groups of the same class. The formation of the lateral fold and then fins development is characteristic of bony fishes. Fins elongation, branchial clefts reduction and lungs development is characteristic of Sarcopterigii. Parallel development of the animal kingdom started with the development of segmentellas about a billion years before the Amphibia appeared [27]. Due to different existence conditions, i.e. environmental temperature, light, food, etc., for related groups of animals the rate of new generations production was different. As a result, aromorphosis were taking place at different times and so the formation of amphibians was diachronous. And when different species of the amphibians and reptiles came out on firm-land it did not happen simultaneously, but took a long period of time.

The development of the animal kingdom is polyphyletic. At early stages of the evolution there were different combinations of aggregated flagellates that were developing in parallel. The polyphyletic origin of the Amphibia is acknowledged by many scientists [19, 20, 21, 29]. This idea should be extrapolated and interpolated over the entire animal kingdom. It is possible to suggest that the origin of the animal kingdom including the vertebrates is polyphyletic and the origin of reptiles and mammals is also polyphyletic i.e. every order of the mammals independently went all the way up the evolution ladder through the stages of fish, Amphibia, and reptiles.

3) Our concept is based on the idea that no organ develops “in order to” perform a function. New organs develop and form according to the laws of development of chromosomes. They can arise from existing structures acquiring new characteristics; and at the same time they can perform a new function, perform less or no work at all and even become a burden. It relates to the development of limbs, axial skeleton, lungs and other organs. An organ with particular characteristics can be an advantage in some new environment, so **natural choosing of the environment** takes place. As for the skeletal system and the limbs in particular, the number of its elements was only decreasing during evolution due to the sequestration of the genetic material. We cannot speak about any new formations here. New organs

cannot appear out of nothing (ad novo). They can arise from existing organs or their parts along with acquiring new functions and becoming independent later. The division of the existing organs takes place in accordance with the symmetry and segmentation common to given type of organisms, that is the quadrilateral symmetry for the vertebrates and 13-segment division for man. Therewith a species being at the start of the evolutionary process may have its organs and bones in particular undeveloped or lacking completely while a species at the end of the evolutionary process often has parts of its organs integrated, reduced or missing.

4) Land invasion by the vertebrates was caused by several factors with the main one being internal changes in the organism according to the consecutive, naturally determined changes of the genetic material. On having acquired lungs and elongated fins the crossopterygian fishes permanently living in inshore waters got an opportunity to use the non-aqueous medium besides their aquatic habitat. When the climate changed they used that opportunity out of necessity. This is how amphibians appeared. Further structural changes led to significant elongation of the limbs that hindered movements in the water.

Those animals whose limbs elongated insignificantly stayed in water and transformed into whales. The myth of the whales returning to water – providing we adhere to the idea of monophyletism – is indefensible as according to Louis Dollo's Law of inconvertibility of evolution a developing species cannot revert back even partly to the previous form. And whales preserved the flukes and interdigital palama, the remnants of the lateral folds, from which limbs arose, and some also have the back fin. According to the monophyletic idea, all these structures are new formations formed out of necessity via natural selection.

Those animals whose limbs though elongated did not hinder their movements in the inshore waters stayed in their habitual environment. The crocodiles can be an example. Animals whose limbs elongated significantly chose fit for habitation environment, i.e. the firm-land. In other words, it was the effect **the law of natural choosing of the environment.**

Organs both appear and disappear irrespective of their functions or the environment, whether or not they are necessary. It is to be supposed that the branchia disappeared due to consecutive changes of the chromosomes (sequestration of the genetic material). Dissolution of the branchia is not the only case of organs vanishing. Other cases are known in biology, viz. complete reduction of teeth in birds while their ancestors had them, vanishing of part of spondylus in some amphibians, legs in some amphibians (limbless amphibians – gymnophiona), reptiles (snakes and some lizards) and some mammals (cetacias).

5) The assessment of congeniality of the fossils and modern animals should be carried out based on their origin and segmentation. One of the ways to establish the congeniality of transitional forms is to thoroughly analyze the number of bones in the limbs and its correlation to the number of bones in the axial skeleton to define the segmentation of the organism. But this is a difficult task as there are precious

few examples of complete skeletons of the fossils.

6) On having their fins changed in a certain way some crossopterygian fishes developing in parallel diverged from their main species and lived in the new form for a long time without further changes. Remains of some of them were preserved in the soil and part of them were found as fossils. Coelacanth (*Latimeria*) can be an example. We believe it is groundless to say the fossils were formed only when the evolutionary changes were taking place; Coelacanth (*Latimeria*) lived millions of years ago and has survived up until now without changes. Not once species having finished their evolution diverged from their developing families. And representatives of some of them can be found now as fossils. As there were a lot of developing species it is incorrect to line up all the fossils as belonging to one and the same species. Since the developmental processes in the species whose fossils are found were parallel it is possible to say there was a general trend for the fish fin to transform into the limb of tetrapods. While assessing the structure of the fossils it should be kept in mind that some bony elements reduced. Only those fossil animals can be considered to be ancestors of some of modern species whose limbs had more bony elements than the modern species' limbs do.

From the point of view of monophyletism, if we find the very first amphibians that started living on firm-land it will give the key to understanding of the origin of all reptiles – ancestors of the mammals. From the point of view of polyphyletism, it does not matter. The origin of the fossils and their belonging to particular species can help us to understand how limbs of the ancestors of man possibly formed and who our potential ancestors were. The fossils of first land animals will be probably found later. It is possible to suggest they will have small sizes.

Structural organization of the organism or its parts, including the limbs, should be assessed not in the context of how necessary they are to perform a function but based on the symmetry, segmentation and internal objective laws. This is what we did in respect to the evolution of human limbs at the very early stages of the development. It appears that no real animal with the extremities constructed according to the above scheme had ever existed by virtue of their unceasing reorganization. Such schemes can be used to elucidate tendencies in evolutionary processes. Osteogenic buds from the continuous lateral fold underwent multiple rearrangements, organization into an octadactyl forelimb and a pentadactyl hindlimb. Further rearrangements of the osteogenic buds in the limbs of remote ancestors of man were related to symmetry processes directed toward building up identical antimeres (pentadactyl limbs). The proposed schemes illustrate different fate of the lateral folds in 5- and 8-segment organisms that provided material for the formation of extremities.

Since the fossil record is not complete we cannot be sure which fossil species could have been the ancestor of man though the surviving breast fin and girdle of *Sauripterus taylori* with two distal rows eight radial elements each similar to the fingers of tetrapods allows us to make specific suggestions. Yet there was an animal whose limb structure confirms our supposition. Figure 2 schematically depicts the extremities of *Acanthostega gunnari* according to J. Clack [22], and the scheme is based on the found

fossils. The limbs structure of *acanthostega gunnari* is clearly seen in the model made by E. Goldfinger, and published by J. Clack [23] with consent of the author (figure 3). The octadactyl forelimb of *Acanthostega gunnari* fairly well fits the proposed scheme. It should be emphasized that the difference in the structure of forelimbs and hindlimbs of *Acanthostega gunnari* also falls in line with our idea. J. Clack interprets arrangement of the bones of the forelimb in different ways. It is related to the fact that there is a variety of ways to adjust the fossils to become a unified complex structure. E. Goldfinger probably had reasons while examining the fossils to arrange them in such order: two rows of five bones each and several rows of eight bones each.

The scheme we offered is not based on examination of the fossils, but on the symmetry and segmentation of the involved animals. This concept of limb skeletal patterns and development will hardly gain immediate recognition. Nevertheless, it appears to be quite correct, taking into account certain pertinent factors:

a) Ancestral mammals are known to have had an additional bone (os acetabulum), besides three other pelvic bones characteristic of modern animals [8, 12, 15]. It can be assumed that the centre of morphogenesis of this bone underwent displacement and gave rise to the second thigh bone. Modern man retained this structure in the form of the sesamoid bone set close to trochanter major;

b) The three bones of the crus: two tibial bones (os tibia, os fibula) and patella (os patella) are a three-component complex of the crus;

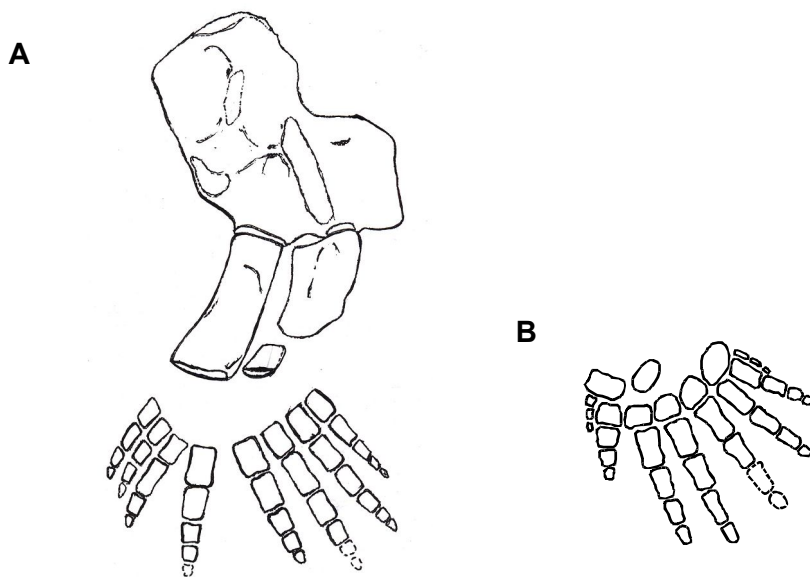


Fig. 2. Reconstruction of the left limbs of *Acanthostega gunnari* according to Clack [22]. A – forelimb; B – hindlimb.



Fig. 3. Model of *Acanthostega gunnari*'s skeleton. The model and photo are made by E. Goldfinger; published by J.A. Clack [23].

c) The proximal row of tarsus consists of two bones: astragalus (os talus) and heel bone (os calcaneus) [11, p. 71]. Occurrence of talocalcaneonavicular joint shows that these two bones are in the same row;

d) The distal part of tarsus is more complex and it is not possible to consider the arrangement of bones in it as an integral row. In this row there is a bone clearly standing out - scaphoid bone (os naviculare); mediate and intermediate sphenoid bones (ossa cuneiforma mediale et intermedium) adjoin it distally. There are two more bones in this part: laterosphenoid (os cuneiformi laterale) and cuboid (os cuboideum), located in between heel bone (os calcaneus) and metatarsal bones (ossa metatarsi). It is possible to suggest that laterosphenoid bone (os cuneiforma laterale), cuboid bone (os cuboideum) and metatarsal bones (ossa metatarsus) where one bone regressed once were making an entire row.

Conclusions

The results of the examination of fossils and the analysis of fin development in tetrapodmorphic fishes, the limbs of tetrapods and also human limbs carries the following inference:

a) None of the species whose representative's remains were found as fossils can be considered to be the very first terrestrial animals; first Amphibia appeared much earlier than the found fossils and traces;

b) The transformation of the fins into the limbs of tetrapods and their development occurred due to regular changes of chromosomes and is not related to the existence conditions;

c) The number of bony elements in the limbs of tetrapods arises from the segment structure of the organism and their reduction ratio during the evolutionary process;

d) Distant ancestors of man were relatives to *Sauripterus taylori* and *Acanthostega gunnari*.

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