UDC 591.471.37:597/599

VARIABILITY OF STRUCTURAL AND BIOMECHANICAL PARAMETERS OF *PELOPHYLAX ESCULENTUS* (AMPHIBIA, ANURA) LIMB BONES

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Variability of Structural and Biomechanical Prameters of *Pelophylax esculentus* (Amphibia, Anura) Limb Bones. Broshko Ye. O. — Structural and biomechanical parameters of Edible Frog, *Pelophylax esculentus* (Linnaeus, 1758), limb bones, namely, mass, linear dimensions, parameters of the shaft's cross-sectional shape (cross-sectional area, moments of inertia, radiuses of inertia) were investigated. Some coefficients were also estimated: diameters ratio (d_f/d_s), cross-sectional index (i_k), principal moments of inertia ratio (I_{max}/I_{min}). Coefficients of variation of linear dimensions (11.9–20.0 %) and relative bone mass (22–35 %) were established. Moments of inertia of various bones are more variable (CV = 41.67–56.35 %) in relation to radii of inertia (CV = 9.68–14.67 %). Shaft's cross-sectional shape is invariable in all cases. However, there is high individual variability of structural and biomechanical parameters of *P. esculentus* limb bones. Variability of parameters was limited by the certain range. We suggest the presence of stable norm in bone structure. Stylopodium bones have the primary biomechanical function among the elements of limb skeleton, because their parameters most clearly responsive to changes in body mass.

K e y   w o r d s: anurans, Edible Frog, locomotion, limbs skeleton, structural and biomechanical parameters, variability, allometry, norm of structure.

Изменчивость структурно-биомеханических параметров костей конечностей *Pelophylax esculentus* (Amphibia, Anura). Брошко Е. О. — Исследованы структурно-биомеханические параметры длинных костей конечностей лягушки съедобной, *Pelophylax esculentus* (Linnaeus, 1758): масса, линейные показатели, параметры геометрии поперечного сечения (площадь компакты, моменты инерции, радиусы инерции). Также вычислены коэффициенты: соотношения диаметров (d_f/d_s), индекс компакты (i_k), соотношение главных моментов инерции (I_{max}/I_{min}). Установлено, что коэффициенты вариации линейных размеров костей составляют 11,9–20,0 %; относительной массы костей — 22–35 %. Сильно изменчивы моменты инерции разных костей (CV = 41,67–56,35 %), в отличие от радиусов инерции (CV = 9,68–14,67 %). На фоне постоянства формы сечения диафиза у всех исследованных особей, о чем свидетельствуют индекс компакты и индекс соотношения диаметров, отмечается высокая индивидуальная изменчивость структурно-биомеханических параметров костей конечностей *P. esculentus*. Однако изменчивость существует в определенных пределах, что позволяет говорить о некой норме структурной организации костей. Ведущую биомеханическую роль среди звеньев скелета конечностей играют стилоподии, параметры костей которых наиболее выражено реагируют на изменения массы тела.

К л ю ч е в ы е   с л о в а: бесхвостые амфибии, лягушка съедобная, локомоция, скелет конечностей, структурно-биомеханические параметры, изменчивость, аллометрия, норма строения.

Introduction

Locomotion of water frogs (Pelophylax) has a dual nature: swimming in the aquatic environment (the primary form of locomotion) and jumping on land (secondary form of locomotion). The activity of hindlimbs, performing the main motor function with the help of cyclic propulsion movements is at the core of both types of locomotion.

Several hypotheses on the origin of terrestrial tailless amphibians jumping locomotion are discussed in the literature (Gans, Parsons, 1966; Sukhanov, 1968): 1) jumping as an adaptation to life on land (Inger, 1962), 2) the occurrence of aquatic primary synchronous propulsion of hindlimbs when swimming, which later could also be used for terrestrial locomotion (Griffiths, 1963), and 3) as an optional method of danger avoiding (Schmalhausen 1964; Gans, Parsons, 1966). The primary tailless amphibians in adulthood were hardly fully terrestrial animals. They were of semi-aquatic lifestyle, so both forms of locomotion could evolve in parallel. In addition, hindlimbs of tailless amphibians do not have significant differences in the overall scheme of kinematics when moving in the water and on land (Nauwelaerts, Aerts, 2003; Nauwelaerts et al., 2005) except their orientation in the horizontal plane when swimming (Sukhanov, 1968). It should be added that the synchrony and symmetry of the limb movements are the most effective way to swim with a shortened trunk and lenghthened limb (Griffiths, 1963; Sukhanov, 1968).

A ground leap of a frog includes the following phases (Nauwelaerts, Aerts, 2006): 1) propulsion (sudden straightening of hindlimbs), 2) flight (with bringing of hindlimbs under the body) 3) landing (amortization on forelimbs), 4) recovery (adoption limbs starting position). Propulsion phase, in turn, comprises two parts (Sukhanov, 1968; Nauwelaerts et al., 2005): 1) extension of the knee joint and 2) extension of ankle and metatarsal joints. At the same time during swimming all the joints act more or less synchronously. Propulsion impact of hindlimbs during a jump is considerably stronger as compared with swimming (Nauwelaerts, Aerts, 2003; Nauwelaerts et al., 2005). Thus, the push force, developed in the first phase of repulsion is 6.5 times higher than that in its second phase (Sukhanov, 1968).

Forelimbs function is in body amortisation in the final phase of the jump. As the surface resistance force when landing on average three times higher than at a push, forelimb bones must also have a sufficient safety margin (Nauwelaerts, Aerts, 2006).

While jumping and swimming at first glance are quite similar in their kinematics, they are used in environments with different density, and hence with different mechanical impact on various parts of limbs. Therefore the distribution of mechanical loads on the elements of the limb should be distinguished. Thus when jumping the proximal limb elements are most involved, and when swimming — distal ones (Nauwelaerts et al., 2007). Because of this, various morphological and functional properties of skeletal limbs reflect adaptation to a particular method of locomotion. Some of them can display adaptation to both types of locomotion, another — only to one of them (Nauwelaerts et al., 2007). We assume that the properties of limb bones significant for both types of locomotion should have a relatively high variability in comparison with those that are relevant for only a single type.

As far as swimming and jumping are realized in different environments, "a conflict of optimization" of locomotion apparatus may occur (Nauwelaerts et al., 2007). Theoretically extension of variability range of limb bones parameters can lead to the animal transition to only swimming or jumping, and accordingly, the existence of adults in definite environment that occur in many species of anurans.

The aim of this work is the investigation of individual variability of structural and biomechanical parameters of long bones of edible frog *Pelophylax esculentus* (Linnaeus, 1758) concerning the changes in body weight, as well as the interrelationship between these characteristics (variability relative to each other). Emphasis is biased towards consideration of adaptations to terrestrial locomotion as in contact with a substrate harder than water limbs skeleton susceptible to mechanical stress more intense than in the aquatic environment.

Material and methods

Skeletal elements of *P. esculentus* of one population (n = 18), namely: bones of stylopodium — humerus and the femur, zeugopodium — forearm bone (os antebrachii), and tibia (os cruris) were studied. The following parameters: bone mass — absolute (m) and the relative body mass (m_r); linear dimensions — length (l), frontal (df) and sagittal (ds) diameters; geometry parameters of mid-diaphyseal cross-section — compact area (Sk), principal (I_{max}, I_{min}) and polar (J) moments of inertia, radii of inertia (i_{max}, i_{min}). Additionally such coefficients: diameter ratio (df/ds), the index of compacts (ik), the ratio of the principal moments of inertia (Imax/Imin) were calculated. To determine the indices of parameters of the diaphyseal bone cross-section geometry special technique was used.

Preview of the section was applied to the grid, where coordinates of individual points on the outer and inner contours of the section were determined. The obtained coordinates were processed with a special computer program (Melnik, Klykov, 1991) for calculation of indicated geometry section parameters (Melnik, Klykov, 1991).

For each of the parameters its average value (M), the rms-parameter deviation (SD), coefficients of variation (CV) and the standard deviation of coefficient of variation (SCV) by standard methods were calculated.

To determine the allometric dependences of each bone parameters on body weight, as well as the diameters of the bones to their length, the equation of nonlinear regression $y = ax^b$, where x — independent variable, y — separate feature index, a — initial growth constant, b — allometric constant was used (Schmidt-Nielsen, 1987; Melnik, Klykov, 1991).

According to generally accepted theoretical calculations, in isometric of parameters to their body mass their allometric constant will be: for bone mass — 1, linear parameters — 0.33, cross-sectional area — 0.67, the

moments of inertia — 1.33. If the corresponding allometric constants larger than these values, it is evidence of an indication as to the positive allometry of body weight, if less — about the negative allometry. Calculations of indicators were done by nonlinear regression with the help of the program SigmaPlot 11.0.

We also calculated the coefficients of multivariate allometry (A) for the set of equivalent one-dimensional features of all bones (separately for bone mass with body weight, relative bone mass, linear dimensions, cross-sectional area, moments of inertia). In this case the estimation of mutual changes in equal parameters is performed. The multivariate allometry coefficient is the ratio of the first principal component factor load on the sign to the arithmetic mean of all loads. Calculating of main component is based on variance-covariance matrix of the log-transformed values (Jolicoeur, 1963, 1984). Here positive allometry characteristics are shown at A > 1, and negative — for A < 1. Calculating of the multivariate allometry coefficient was performed using the program PAST (Hammer et al., 2001).

Results and discussion

The cross-sectional shape of the bones. Cross-sectional shape of the limb bones illustrates their adaptation to loads of different character. Thus, hindlimb bones (femur and shin bone) have a round cross-sectional shape (fig. 1, *C*, *D*), indicating the adaptation of the latter to bending and torsion, and is associated with segmental position of limbs in amphibians. Although the basic movements of the hindlimb are exercised along the sagittal plane, the rotation around the front axis (especially of the femur) is also presented.
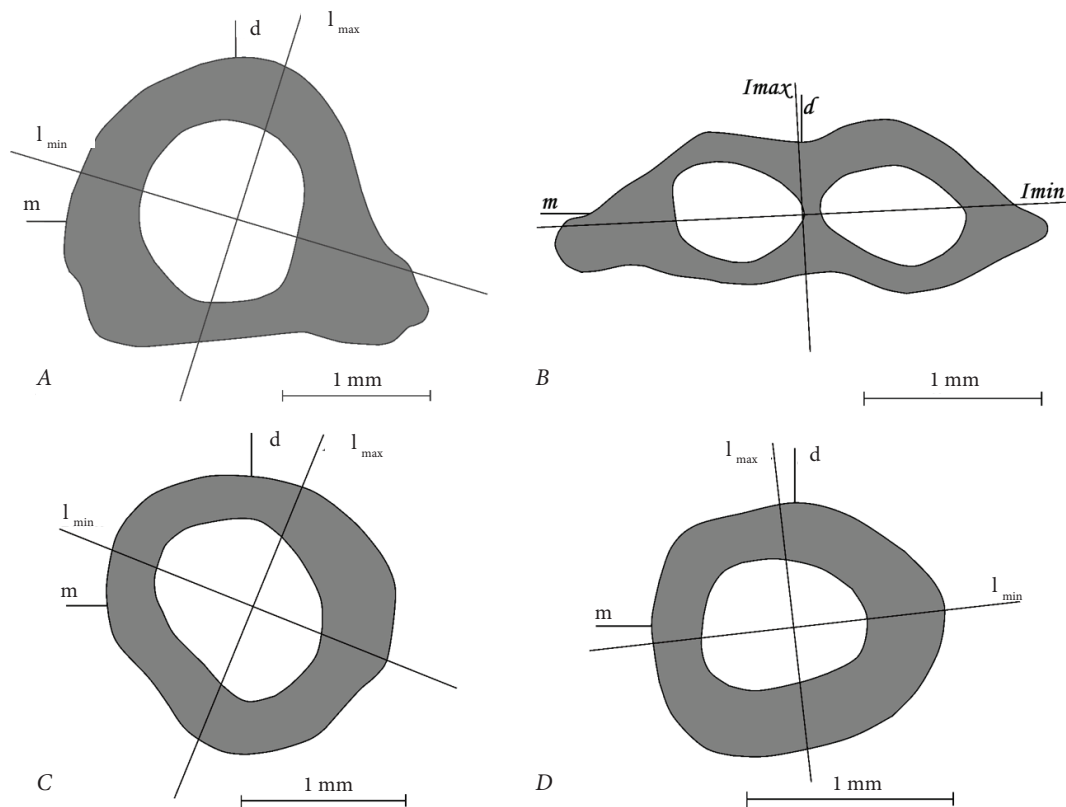

Fig. 1. Shaft's cross-sectional shape of *P. esculentus* long bones: *A* — humeral; *B* — forearm; *C* — femoral; *D* — crural (d — dorsal mark; m — medial mark; I_{max} — maximum moment of inertia axis; I_{min} — minimum moment of inertia axis).

Рис. 1. Форма поперечного сечения диафиза длинных костей конечностей *P. esculentus*: *A* — плечевой; *B* — кости предплечья; *C* — бедренной; *D* — кости голени (d — дорсальный маркер; m — медиальный маркер; I_{max} — ось максимальных моментов инерции; I_{min} — ось минимальных моментов инерции).

Cross-sectional shape of the humerus is extended in the frontal plane (fig. 1, *A*), indicating more intensive bending loads in the frontal plane due to the damping function of the bone (acting as a lever) in the final phase of the jump.

The forearm bone also has features of adaptation to loads in this phase, resulting in a fusion of two primary elements (ulna and radius) with forming a coherent rigid structure (fig. 1, *B*).

O v e r a l l   p a r a m e t e r s   v a r i a b i l i t y   o f   l i m b   b o n e s . Overall in *P. esculentus*, a rather large variability of the studied parameters (table 1; fig. 2) is observed. Unfortunately, published data on the variability of structural and biomechanical parameters of bone in tailless amphibians are virtually unknown.

Determined coefficients of variation of the linear dimensions of *P. esculentus* limb bones constitute 11.9–20.0 %. Whereas according A. V. Yablokov (1966), variability of linear parameters of skeletal elements in mammals is 3–10 %. Variability of the relative bone mass of frog (CV = 22–35 %) is also higher than in mammals, average 10–20 % (Yablokov, 1966).

It should be also noted that, according to our data, the parameters of geometry of the diaphysis cross section (especially the moments of inertia) are generally very variable val-

T a b l e   1. Variability of bone parameters of *P. esculentus*

Т а б л и ц а   1. Изменчивость параметров костей у *P. esculentus*

Parameter	M	SD	Lim	M	SD	Lim
	Humerus			Os antebrachii		
m, g	0.14	0.06	0.05–0.23	0.04	0.02	0.012-0.075
m_r	0.0018	0.0005	0.001–0.0027	0.0006	0.00015	0.0003-0.0008
L, mm	21.4	2.9	16.7–25.7	11.5	1.4	8.9–13.8
d_p, mm	2.3	0.3	1.6–3	2.6	0.4	1.9–3.2
d_s, mm	2	0.3	1.6–2.4	1	0.2	0.7–1.6
d_r/d_s	1.14	0.14	0.94–1.38	2.78	0.38	1.94–3.5
S_k, mm^2	2.01	0.64	0.82–3.1	1.17	0.28	0.77–1.64
i_k	0.53	0.09	0.36–0.69	0.54	0.07	0.4–0.65
I_{max}, mm^4	1.26	0.71	0.3–2.89	0.71	0.36	0.27–1.43
I_{min}, mm^4	0.69	0.33	0.2–1.48	0.12	0.05	0.05–0.21
I_{max}/I_{min}	1.8	0.41	1.25–2.58	6	1.4	3–8.71
J, mm^4	1.95	1.01	0.5–4.01	0.82	0.4	0.35–1.64
i_{max}, mm	0.76	0.1	0.6–1	0.75	0.11	0.58–0.99
i_{min}, mm	0.57	0.06	0.45–0.69	0.31	0.03	0.26–0.38
	Femur			Os cruris		
m, g	0.29	0.12	0.115–0.5	0.32	0.12	0.135–0.51
m_r	0.0038	0.0008	0.0022–0.005	0.0041	0.0008	0.0028-0.0055
L, mm	36.5	4.8	27.5–44	39.5	4.7	32.1–47
d_p, mm	1.9	0.3	1.4–2.3	2.3	0.3	1.6–2.7
d_s, mm	1.9	0.3	1.4–2.3	1.9	0.3	1.4–2.3
d_r/d_s	1	0.04	0.91–1.06	1.23	0.09	1.04–1.42
S_k, mm^2	2.18	0.59	1.13–2.85	2.86	0.74	1.69–3.85
i_k	0.69	0.08	0.55–0.82	0.77	0.06	0.66–0.89
I_{max}, mm^4	0.83	0.37	0.3–1.45	1.39	0.63	0.44–2.49
I_{min}, mm^4	0.67	0.29	0.21–1.13	0.86	0.39	0.29–1.52
I_{max}/I_{min}	1.24	0.14	1–1.45	1.64	0.29	1.41–2.5
J, mm^4	1.5	0.66	0.51–2.56	2.26	1.01	0.73–3.82
i_{max}, mm	0.6	0.07	0.51–0.72	0.68	0.09	0.5–0.81
i_{min}, mm	0.54	0.06	0.43–0.63	0.53	0.07	0.41–0.65

N o t e. Variability of body mass: M = 76.5 g; SD = 25.35 g; CV = 33.14 %; S_{CV} = 7.82; Lim — 43–136 g.
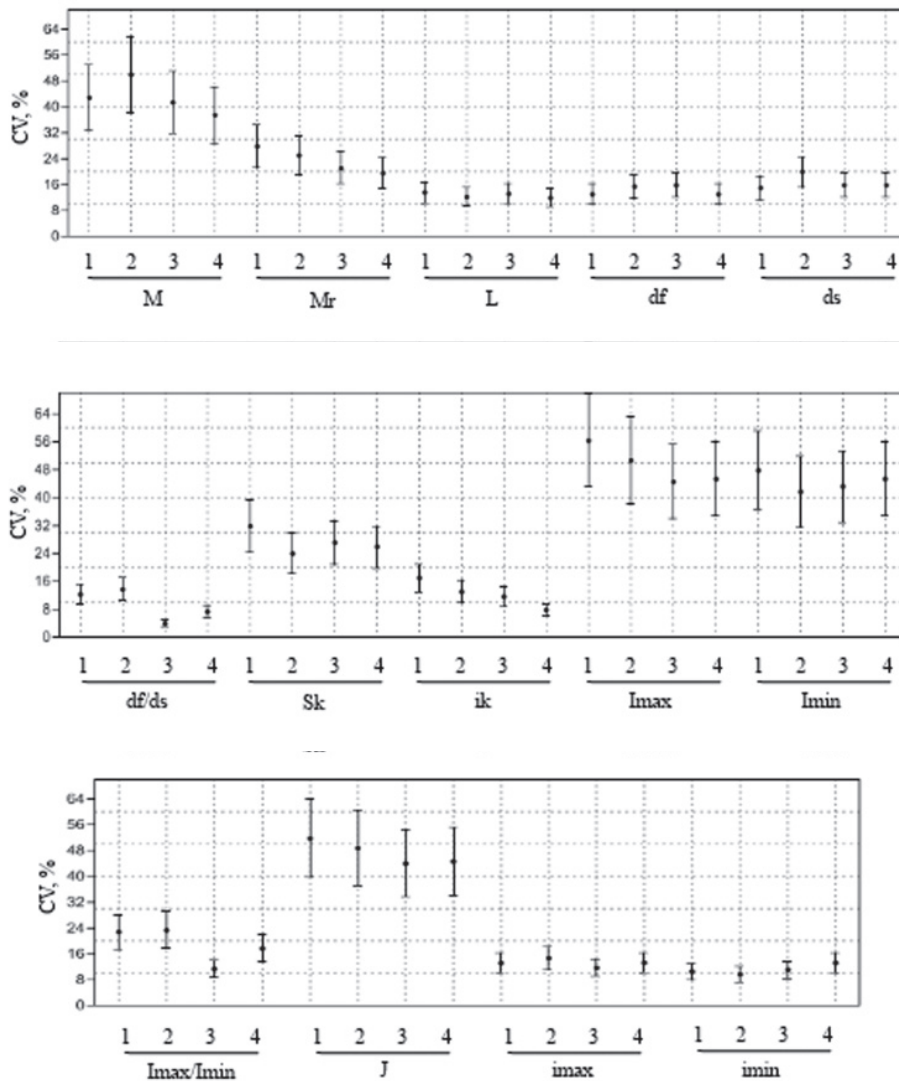
Fig. 2. Coefficients of variation (CV) of morphometric and biomechanical parameters of *P. esculentus* limbs' long bones (1 — humeral; 2 — forearm bone; 3 — femoral; 4 — crural bone).

Рис. 2. Коэффициенты вариации (CV) морфометрических и структурно-биомеханических параметров длинных костей конечностей *P. esculentus* (1 — плечевая; 2 — кость предплечья; 3 — бедренная; 4 — кость голени).

ues (CV = 41.67–56.35 %). To a lesser extent it concerns the radii of inertia, which are the linear dimensions of the diaphysis cross section (CV = 9.68–14.67 %). It is likely that these parameters will have a high variability in other animal species.

The high individual variability of the species and morphological characteristics of the postcranial skeleton of Anura is described in papers of E. E. Kovalenko (2011). This author, on the basis of a range of possible options for the structure of the body, marks out its norm - the most common variants. In our case, the individual variability of structural and biomechanical parameters of P. *esculentus* limb bones is quite high (fig. 2). In this case the diaphysis cross-sectional shape in all individuals remains constant in accordance with its adaptations to a certain kind of mechanical load.

Based on the foregoing, and works of E. E. Kovalenko in particular, we can speak of a sustainable limb bones building standards in *P. esculentus*, and the high variability of com-

T a b l e 2. Allometric dependencies of bone parameters on body mass

Т а б л и ц а 2. Аллометрические зависимости параметров костей от массы тела

Parameter	a	b	S_b	r	a	b	S_b	r
	Humerus				Os antebrachii			
m	4.006	1.348	0.204	0.823	0.524	0.963	0.175	0.828
l	56.27	0.374	0.048	0.888	27.37	0.335	0.036	0.921
d_f	5.341	0.331	0.075	0.738	6.591	0.363	0.06	0.838
d_s	4.61	0.322	0.065	0.782	2.06	0.311	0.097	0.624
S_k	1.077	0.712	0.249	0.557	4.035	0.473	0.138	0.671
I_{max}	34.38	1.442	0.434	0.57	7.945	0.934	0.304	0.626
I_{min}	10.96	1.185	0.324	0.628	1.054	0.849	0.24	0.68
J	45	1.353	0.386	0.598	8.972	0.922	0.29	0.639
i_{max}	1.413	0.245	0.083	0.59	1.29	0.207	0.099	0.471
i_{min}	1.027	0.229	0.057	0.708	0.477	0.164	0.072	0.501
	Femur				Os cruris			
m	6.584	1.247	0.162	0.866	5.727	1.155	0.141	0.884
l	96.17	0.374	0.038	0.925	88.47	0.312	0.041	0.886
d_f	4.489	0.329	0.067	0.778	5.958	0.374	0.058	0.853
d_s	4.974	0.367	0.067	0.81	4.113	0.312	0.08	0.703
S_k	16.33	0.796	0.111	0.868	14.3	0.644	0.123	0.793
I_{max}	15.56	1.202	0.188	0.825	33.68	1.307	0.209	0.823
I_{min}	14.01	1.245	0.192	0.831	8.338	0.984	0.252	0.682
J	29.47	1.218	0.185	0.834	41.84	1.212	0.221	0.788
i_{max}	1.051	0.221	0.061	0.676	1.431	0.294	0.066	0.744
i_{min}	0.95	0.223	0.064	0.659	0.854	0.189	0.081	0.508

N o t e. Here, and in table 3 and: a — constant initial growth; b — allometric constant; Sb — standard error of b; r — the correlation coefficient.

pact area and moments of inertia — is among other things a manifestation of individual morphological features, which, however, do not go beyond the norm, as are compensated by stability form of the diaphysis cross section.

To assess the constant cross-sectional shape compact index and indexes diameter ratio and principal moments of inertia ratio are indicative, showing in this case a relatively small variation, which confirms the existence of some rules in the structure of bones. Relatively broad scope of "normal structure" is in the forearm bone due to the high variability of its frontal diameter. Accordingly, the higher variability is shown for the ratio of its diameters.

A l l o m e t r i c p a r a m e t e r s d e p e n d e n c e s. Mass and linear dimensions of limb bones have a high correlation with body weight (r > 0.7; table. 2). Also it can be traced to the

T a b l e 3. Allometric dependencies of bone diameters on bone length

Т а б л и ц а 3. Аллометрические зависимости диаметров костей от их длины

Parameter	a	b	S_b	r	a	b	S_b	r
	Humerus				Os antebrachii			
d_f	0.259	0.706	0.188	0.69	0.223	1	0.161	0.847
d_s	0.157	0.831	0.138	0.837	0.092	0.941	0.257	0.679
	Femur				Os cruris			
d_f	0.058	0.971	0.108	0.917	0.049	1.042	0.151	0.868
d_s	0.055	0.987	0.129	0.891	0.029	1.134	0.158	0.875

parameters of cross section geometry of hindlimb bones. For forelimb bones these options have an average level of correlation (r = 0.5–0.7).

In assessing the null hypothesis for the allometric constants is revealed that their values do not exceed the limits of confidence intervals variation.

This can indirectly testify of signs isometric to body weight. But the experience of many researchers shows that, in determining the dependency of the relative parameters growth should be guided by the averages values of allometric constants. Allometric constants of bone parameters relative to body mass indicate the varied nature of the dependency (table 2). Thus, the lengths and diameters of the most bones vary isometrically with the exception of the forearm, where a negative allometry in all respects is observed.

The latter indicates that changes in body weight are not determining factor for forearm, since by its sophisticated design, it is quite stable. In other respects these tendencies can be traced according to body weight: positive allometry of bone mass, negative allometry radii of inertia and positive allometry for stylopodium bones compact area.

T a b l e 4. Coefficients of multivariate allometry of bone mass and body mass

Т а б л и ц а 4. Коэффициенты многомерной аллометрии массы костей и тела

Parameter	A	2.5 %	97.5 %
M_{body}	0.7146	0.5558	0.9652
$M_{humerus}$	1.119	0.9909	1.235
$M_{os\ antebrachii}$	1.102	0.8568	1.277
M_{femur}	1.071	0.9831	1.154
$M_{os\ cruris}$	0.9937	0.9165	1.074

N o t e. Contribution of the 1st principal component to the total variance PC1Var = 92.52 %. Here, and in table 7–10: 2.5 % and 97.5 % — confidence limits.

T a b l e 5. Coefficients of multivariate allometry of relative bone mass

Т а б л и ц а 5. Коэффициенты многомерной аллометрии относительной массы костей

Bone	A	2.5 %	97.5 %
Humerus	1.217	1.007	1.768
Os antebrachii	1.11	0.5215	1.354
Femur	0.9035	0.6826	1.006
Os cruris	0.7687	0.6268	0.9642

N o t e. Contribution of the 1st principal component to the total variance PC1Var = 81.15 %.

T a b l e 6. Coefficients of multivariate allometry of bones linear dimensions

Т а б л и ц а 6. Коэффициенты многомерной аллометрии линейных размеров костей

Parameter	Bone	A	2.5 %	97.5 %	Bone	A	2.5 %	97.5 %
l	Humerus	1.104	0.8948	1.38	Femur	1.129	0.9273	1.336
	Os antebrachii	0.9407	0.667	1.177	Os cruris	0.9858	0.8034	1.223
d_f	Humerus	0.7377	0.2677	1.418	Femur	1.208	0.9463	1.426
	Os antebrachii	1.181	0.866	1.426	Os cruris	1.168	0.8599	1.373
d_s	Humerus	1.067	0.7953	1.405	Femur	1.252	1.028	1.457
	Os antebrachii	1.239	0.6323	1.945	Os cruris	1.218	0.8196	1.565
i_{max}	Humerus	0.914	0.5712	1.38	Femur	0.915	0.6959	1.198
	Os antebrachii	0.7089	0.1726	1.141	Os cruris	1.052	0.7212	1.259
i_{min}	Humerus	0.7238	0.4593	1.175	Femur	0.8967	0.6239	1.149
	Os antebrachii	0.6324	0.2613	0.9521	Os cruris	0.9269	0.4807	1.236

N o t e. Contribution of the 1st principal component to the total variance PC1Var = 71.94 %.

T a b l e 7. Coefficients of multivariate allometry of bones cross-sectional area

Т а б л и ц а 7. Коэффициенты многомерной аллометрии площади компакты костей

Bone	A	2.5 %	97.5 %
Humerus	1.158	0.7136	1.53
Os antebrachii	0.8342	0.7068	1.097
Femur	1.092	0.9103	1.298
Os cruris	0.9152	0.645	1.193

N o t e. Contribution of the 1st principal component to the total variance PC1Var = 80.85 %.

T a b l e 8. Coefficients of multivariate allometry of bones moments of inertia

Т а б л и ц а 8. Коэффициенты многомерной аллометрии моментов инерции костей

Parameter	Bone	A	2.5 %	97.5 %	Bone	A	2.5 %	97.5 %
I_{max}	Humerus	1.096	0.7152	1.522	Femur	1.057	0.8885	1.255
	Os antebrachii	0.9033	0.6446	1.195	Os cruris	1.08	0.8506	1.299
I_{min}	Humerus	0.9682	0.6507	1.304	Femur	1.061	0.8432	1.253
	Os antebrachii	0.7936	0.5903	1.007	Os cruris	0.9934	0.6766	1.277
J	Humerus	1.052	0.712	1.428	Femur	1.058	0.8757	1.245
	Os antebrachii	0.887	0.648	1.15	Os cruris	1.051	0.805	1.277

N o t e. Contribution of the 1st principal component to the total variance PC1Var = 81.03 %.

In the study of allometric dependencies of diaphysis diameters to the length of the humerus bone negative diameters allometry is clearly expressed, for the other bones this dependence is close to isometry (table 3).

We conclude that stylopodium play a leading role in the bio-mechanics of the frogs' limbs as the femur and the humerus most likely respond to changes in body weight.

This manifests itself in a positive allometry to body weight of these bones lengths and geometry parameters of the humerus section.

Overall, these results are consistent with the available literature data describing the relationship of the studied parameters on the interspecific level in mammals. Thus, the linear dimensions of isometry of bone corresponds to the model of geometric similarity (McMahon, 1975). Deviations from geometry parameters isometry of section are described by the elastic similarity model justifying their dependence on the elastic properties of bone (Alexander, 1977). This indicates the possibility of using allometry methods for studying the intraspecific variation.

Multivariate parameters allometry. Multivariate mass indices allometry (body and separate bones; table 4) shows a significant negative allometry of body mass relative to bone mass (A = 0.715), a small positive allometry for the forelimb bone (1.102–1.119), and isometry for hindlimb bones (0.994–1.071).

These data are consistent with the data of simple allometry, where the bone mass has a positive allometry relative to body weight. This is probably indicative of a more intensive increase in mechanical load on the skeleton limbs relative to body weight gain.

For the relative weights of the limbs skeleton elements a tendency toward positive allometry for forelimb bones (1.11–1.217), the negative allometry for hindlimb bones (0.769–0.904; table 5) were recorded. Thus for the tibia bone negative allometry is quite high (0.769).

Linear bone parameters (length, diameter, radius of inertia (table 6) have the following ratios: positive allometry of stylopodium length (1.104–1.125) , the figures closed to isometric — for the zeugopodium length (0.941–0.986) expressed positive allometry (1.067–1.252) all diameters (except a frontal diameter of the humerus , where a pronounced negative allometry is observed (A = 0.738); negative allometry radii of inertia (0.632–0.927) .

For cross-sectional area (table 7) positive allometry for stylopodium bones (1.092–1.158), negative — for zeugopodium bones (0.834–0.915) are observed.

According to multivariate allometry moments of inertia (table 8) isometry in all bones (0.968–1.096) is observed, only in the forearm it is negative (0.794–0.903).

In general, mutual allometry of homologous parameters of different bones coincides with the results of simple allometry signs to body mass. So, for stylopodium higher relative growth of linear parameters and compact area are also marked, for the forearm — the lower growth of the moments of inertia is noted.

Conclusion

Analyzing the morphometric and structural — biomechanical parameters of skeleton limbs elements of *P. esculentus* and their variability, we obtain the following generalizations.

Retaining the relative stability of certain parameters on the background of elevated variability of others the Anura limbs skeleton achieved the desired balance of its structure: it does not lose its adaptations to aquatic locomotion and gained stability to excess mechanical load accompanying terrestrial locomotion .

A certain range of variability inherent in different structural and biomechanical parameters of the limbs skeletal elements of *P. esculentus*.

Meanwhile variability is present in certain limits, without going out the boundary of the extreme values, which suggests to talk about a certain norm of structural organization of the bones associated with both habitat conditions and characteristics of locomotion.

Existing range of variability of separate parameters are considered as saving the potential for the realization of other ways of adaptive evolution in the case of changes in living conditions.

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