

## **The role of ecological and phylogenetic factors in the problem of interspecific metabolic allometric scaling**

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### **Abstract**

The problem of interspecific allometric scaling can be formulated as finding fundamental causes, why the metabolic rate increases slower than mass. It is still considered as unsolved one. Scientists presently agree that there is no universal value of allometric exponent (a previously popular proposition), and that the phenomenon rather depends on combination of different factors. Otherwise, the progress in solving this problem has rather stalled. In the last two decades, a trend of transforming real data into a virtual space by accounting for phylogenetic dependencies took place. However, such studies did not advance understanding of fundamental mechanisms. Instead, things became even more uncertain, and the whole body of previous studies was jeopardized as non-conforming to phylogenetic corrections, although the only result the phylogenetic approach produced so far is that the corrected allometric exponents produce irregular patterns, and that the problem is difficult to solve. Here, we analyze two approaches: 'phylogenetic correction', and direct accounting for ecological and other factors. We show that phylogenetic approach has inherent methodological mathematical and conceptual flaws, which misled its followers to believe in its supremacy, compared to more traditional methods. We suggest more measurable approach: accounting for different factors, use real data (unless it is proved that some transformation is necessary), allowing consideration of alternative non-phylogenetic approaches, and returning into consideration the body of previous works. In our opinion, together, these measures will provide a solid base for advancing the subject and solving the problem.

**Key-words:** metabolism; allometric scaling; ecological factors; phylogenetic correction

### **Introduction**

The effect of slower increase of metabolic rate (the amount of energy produced per unit time) compared to mass increase was discovered in 19-th century by Rubner. In 1932, Kleiber (1932) introduced a qualitative description of the phenomenon, using a power function in the form of  $B = aM^b$ , where  $a$  is a constant,  $M$  is mass, and  $b$  is the allometric exponent. He also obtained a value of  $b \approx 0.74$ , and, for convenience, rounded it to  $0.75=3/4$ . Such a round value, in the view of people, implicitly assumed some universal fundamental mechanism underlying the phenomenon. The perception certainly influenced the following studies, attempting to explain this value and the nature of the phenomenon.

From an idea of a single universal value of allometric exponent (two most popular values were considered,  $3/4$  and  $2/3$ ), researchers came to a consensus that there is no a single universal value, but the phenomenon is defined by combination of factors, whose different compositions produce different allometric exponents. Certain hierarchical sets of these factors were proposed. Two major schools of thought originated on this ground. One assumes the influence of both ecological and phylogenetic factors, giving priority to ecological factors, when adaptation mechanisms are of greater importance for the species survival than historically acquired features

(expressed as phylogenetic dependencies). The "phylogenetic" camp exhibits rather unilateral approach, transforming all data through the so called "phylogenetic correction", using phylogenetic trees, and then studying the observed allometric effects on the basis of this modified data. Compared to conventional approaches, thus obtained data generally exhibit less regularity across taxa, compared to allometric exponents found by conventional approaches. Such data virtualization made their interpretation more difficult and substantially less certain. The result is that these two visions, representing different sides of the same phenomenon, instead of collaboration are positioned as the opposite approaches, mostly due to implacability of phylogenetic adherents.

Ecological approach produces more credible results. In particular, it showed that the mass's increase is responsible for the main change of metabolic rate, while other factors explain residual values. For instance, McNab (2005) obtained that "Most of the variation (98.8 %) in basal rate of metabolism (BMR) in 70 species of marsupials is correlated with body mass". Many similar studies discovered analogously convincing results. So, ecological factors, at least, should not be disregarded.

The phylogenetic approach produced two main outputs. First, accounting for phylogeny produces a better data fit for transformed data (but a substantially greater divergence of values of allometric exponents). However, as we will discuss, this effect of a better data fit is a consequence of the properties of mathematical procedures, which on average, indeed, provide a better fit, but the actual phylogenetic information has little to do with this effect, save for the always positive correlation of considered traits. In particular, in case of "generalized phylogenetic least squares" (PGLS) method, this happens because of the *always positive* terms of the covariance matrix describing phylogenetic dependencies. The second result is that the allometric exponents obtained with the aid of phylogenetic trees exhibit great variability, for which there are no reasonable explanations. This result is especially discouraging with regard to finding fundamental causes of allometric scaling, since such high variability, which cannot be traced to particular mechanisms, effectively makes such a task impossible, which some adherents acknowledge. Despite these controversies and lack of progress, not to say advantages, the phylogenetic approach received better support in recent years, apparently due to its novelty, "scientifically" looking complicated mathematical methods, and one-sided *conceptual* simplicity, converging the richness, adaptive and evolutionary diversity of nature to a single factor, which can be easily and mechanically applied to any such problem without giving much thought about methods' applicability, as well as validation of obtained results.

So, in this paper, we explore both approaches from the perspective of solving the main problem - their suitability for finding fundamental causes of interspecific allometric scaling.

## **Methods and Discussion**

### **The purpose of allometric studies and methodology**

The goal of allometric studies is to understand the mechanisms (especially fundamental ones) and factors underlying this phenomenon, and their hierarchy and relationships. Such knowledge, in turn, will help understanding physiology, evolution, ecology and organization of living organisms (in organismal and population dimensions), with further influences on practical

applications in medicine, biology, agriculture, environment, industrial applications, etc; in other words, making the humankind lot better through scientific advances.

Scientific studies of this kind traditionally rely on experimental observations, which are then used as the basis for deductions and generalizations uncovering the inner mechanisms and properties of the studied phenomena. Then, this knowledge can be used in different ways, such as planning the next round of more focused experiments, with the following analysis, thus iteratively and incrementally approaching the required level of understanding and adequacy.

Interpretation of scaling relationships, which represent the summary effect of different factors, is a delicate issue. Taylor and Thomas (2014) say in this regard: "problems stem from the fact that empirical scaling relationships in biology are, at best, bivariate approximations of multivariable phenomena. This has important consequences for the statistical methods that can be used and for the inferences that we can draw. In particular, it means that we should not treat a bivariate scaling relationship as if it estimated the parameters of an underlying multivariable physical model." In other words, the quote emphasizes the inherently multifactor nature of interspecific allometric scaling.

Acquiring a reliable knowledge, one can create adequate predictive and descriptive models of the phenomenon, which can be used for practical and scientific purposes. General methodological approaches and concepts for creating models are discussed in (Shestopaloff 2014), using an example of modeling liver metabolism. The success of the cited study, as well as others based on those methodological concepts, confirms their practicality and validity. In brief, these concepts are as follows.

1. Models' core properties should reflect on *real* biological mechanisms, with as little abstraction layers as possible.
2. The best approach to modeling is on the basis of real *fundamental* mechanisms.
3. Models' verifiability is of the highest priority, which includes experiments and all other possible direct and indirect verification, up to the general and philosophical principles.
4. Priority should be given to models incorporating directly measured parameters.
5. Unless the inherent nature of some phenomenon is stochastic, priority has to be given to deterministic models, since they provide more clarity and control, and better exhibit the nature of phenomena.
6. Models should have enough constraints, at all spatial levels, to reduce or remove ambiguity, and make their application feasible for practical purposes and further studies.
7. Models should have a well defined and coherent structure uniting its components.
8. Models should adhere to a multiscale and multifactor cognitive paradigm, without exclusion of potentially meaningful factors, unless it is proved otherwise (like unjustified a priori exclusion of ecological factors in phylogenetic analysis).
9. "Vertical" integration models (meaning inclusion of different scale levels) should be of higher priority. The model's initial structure should allow adding more components at each scale level.

As one can see, this approach encourages the use of direct measurements, where appropriate; considering multiple factors in their interrelationships, different spatial levels, applying constraints, which enhance models' unambiguity. The strongest emphasis is given to *verification* and *validation* of models. Unfortunately, phylogenetic approach fails on each item in this list, and especially on validation and verification of the approach itself and obtained results. Twenty

years of phylogenetic analysis in allometry, by and large, produced no results which could shed light on the core nature of interspecific allometric scaling. Rather, the opposite happened: all previous results and explanations accumulated since the first Kleiber's work were discarded as invalid, while introduction of phylogenetic dependencies led to such a great variety and range of allometric exponents, that it just became impossible to find any regularity in such a scattered pattern. Thus, the implicit mood with regard to solving the problem became rather pessimistic. Such, White and Kearney (2012) wrote: "However, if the non-isometric scaling of metabolic rate *is ever to be understood* (italics is mine), it is first necessary to know exactly what the relationship is. Recent metaanalyses ... have failed to support any single value of the allometric scaling exponents relating BMR to body mass." Note that the quote refers mostly to analysis based on phylogenetic trees, while the studies considering ecological approach and multiple factors, produce encouraging and meaningful results.

In fact, there are very reasonable approaches to the problem and plausible explanations of mechanisms underlying metabolic allometric scaling, such as (Westoby et al. 1995; McNab 2005, 2006, 2008, 2009, 2010; Shestopaloff 2016a, 2016b, 2016c) and many others, but those studies exercise more cautious approach towards phylogenetic approach, and so the phylogenetic school of thought, as usually all extreme teachings do, ignores them entirely. It would be more appropriate to allow such authors sharing results of their studies with the community, than declaring the phylogenetic paradigm as an absolute and unquestionable truth.

### **Accounting for phylogeny in comparative physiology studies**

The idea was introduced in (Felsenstein 1985); further developed in (Capellini et al. 2009; Garland et al. 2005; Garland and Ives 2000; Martins and Hansen 1997; White et al. 2009) and other works. It postulates that data related to allometry depend through common ancestry, and so this dependency should be accounted through phylogenetic trees, for which purpose mathematical methods were proposed. Other factors, by and large, are not considered. The idea and its implementations have certain weaknesses and ignore several important facts and realities. Few of them are as follows.

- (a) The organismal properties depend not only on phylogenetic history, but very much are shaped by ecological and other factors.
- (b) Phylogenetic information is often ambiguous; it is difficult to obtain it, and even more difficult to verify. Especially the worrisome fact is that the results obtained this way are practically impossible to validate.
- (c) The influence of different factors during periods, corresponding to phylogenetic branches, is not uniform in intensity, so that the branch length is not an adequate measure of phylogenetic divergence. Some newer methods allowing for the use of (still rather subjective) ad hoc adjustments, but they do not principally remedy the situation.
- (d) Mathematical methods do not represent an adequate description of the phenomenon. For instance, in the limit, they produce inadequate results, such as the zero confidence intervals or identical and equalized data points.

Let us consider some argumentation of the proponents of phylogenetic methods. Capellini et al. (2010) wrote about previous studies using phylogenetic trees the following: "Hence, it is currently unclear whether variability in scaling exponents reflects *methodology or biological*

*reality*" (italics is mine). In order to overcome this uncertainty, they proposed a modification, which, in their opinion "unlike OLS and PIC, PGLSk does not impose a given value for the phylogenetic signal on the data, but it finds the best-fitting model with the appropriate "lambda" value that could range from 0 to 1".

The problem with this and similar approaches is that they use an invalid implicit assumption that the best data fit automatically means the most truthful and trustful result. In fact, this just means that one managed to find a combination of parameters that provides a better data fit among other alternatives, for this particular mathematical apparatus and for a particular set of assumptions; not more than that. In order to claim the truthfulness for such a result, the validation by other *independent* means, and by experimental data at the first place, is required. Until this is done, nothing can be said. From the viewpoint of scientific methodology and theory of verification of scientific knowledge, this is a deeply flawed approach. So, the question "*methodology or biological reality*" remains unanswered. The verification problem is aggravated by the fact that phylogenetic approach requires to transform *all* experimental data by the *verified* method, which makes such experimental validation extremely difficult, if not impossible.

The main argument in favor of phylogenetic approach, which unconditionally fascinates its followers for the last twenty years, is a better data fit, or adjustable confidence intervals, produced by their procedures. Capellini et al. (2010) expresses this view as follows: "Because PGLSk models better fit the data, conclusions on the theoretical values of the allometric slopes of metabolic rates should be based on such models rather than on non-phylogenetic OLS or PIC models". And further, "PGLSk models, that account for the phylogenetic signal in the data, *always* (italics is mine) fit the data better than OLS models and PIC and should therefore be preferred when studying the allometry and evolution of metabolic rates."

Similar views were expressed in (White et al. 2009; Lovegrove and Mowoe 2014; Garland et al. 2005). In other words, the verification of the concept and particular models, and the results, by and large was reduced to a better data fit. This is a unilateral and deeply erroneous approach. What if a certain degree of diversion is an inherent property of the phenomenon in hand, or there are other unaccounted factors acting in a similar way? Garland et al. (2005), although adamant proponents of phylogenetic approach, show more reasoning in this regard and acknowledge that "finding a model that fits a set of data reasonably well does not necessarily mean that it is the correct model, and other models can probably be found that would provide equally good fit". The said nullifies the main and, by and large, *the only* argument in favor of phylogenetic approach.

### **Mathematical pitfalls of phylogenetic approaches**

Let us turn to mathematical specifics of phylogenetic methods. Capellini et al. (2010) suggest finding phylogenetic signal from the data fitting procedure, which, as we showed above, is an erroneous approach. However, even if we disregard such a mathematical interplay, whose applicability was not validated, the essence of all mathematical phylogenetic methods is using some apriori information to change the actual input data. Such mathematical procedures, indeed, could provide better statistical inferences, provided certain conditions are met, of which the main ones are that the accounted dependencies are *the only ones* affecting input data, and that the dependencies are described *correctly*. None of these conditions is fulfilled in case of phylogenetic analysis. Neither anybody can claim that phylogenetic dependencies are definitive and accurate enough for such applications (Garland et al. 2005; Capellini et al. 2010; White and

Kearney 2012), since no such validation was done. Even worse, there is no way to do such a general validation. Few sporadic results, which can be easily questioned, make no difference.

In case of ecological factors, the situation is much more robust in this regard. It was shown in (Westoby et al. 1995; McNab 2005, 2006, 2008, 2009, 2010; Shestopaloff 2016a, 2016b, 2016c) that ecological and other factors are of great importance and explain much of the observed allometric effects.

Even much simpler and deterministic physical phenomena may have very different interpretations depending on chosen mathematical apparatus, as the work (Shestopaloff 2011) showed. From a mathematical perspective, what we have in case of phylogenetic approach, is the imposition of *always positive* correlation of certain values, presented in a form of a covariance matrix. Transformation of such a matrix into a diagonal form, and then applying the transformation matrix to original data, on average, *has to* produce a less sparse data. This is not a matter of 'if', but 'how significantly less'. (*This* mathematical property of the procedure is *the only* reason why Capellini et al. (2010) '*always*' obtained better data fit, as well as other authors. The phylogeny just supplies always positive correlation coefficients, which otherwise can be arbitrary, this is it.) Note that in the limit, when all input data are entirely dependent, such a procedure pulls all data together. All variability in this case is entirely defined by the imposed constraints and assumptions. This argument can be refuted by a preposition that what is happening in the limit is not applied to what is in the middle. In fact, choosing an appropriate norm, it is possible to show a *uniform* convergence to such a limit for a wide range of initial conditions.

The said about mathematical specifics of methods used in phylogenetic analysis, and their *principle* property of reducing divergence of *just positively correlated* parameters, on average, found confirmation in the studies of proponents of phylogenetic methods too. Such, Garland and Ives (2000) obtained that "In the limit, if the hypothetical species were attached infinitely close to the sister tip, then the prediction intervals would diminish *to 0* (*italics is mine*)", which is effectively the same effect of convergence of all data we discussed before; just the mathematical implementation of the same idea is slightly different, allowing for manipulation of confidence intervals. Garland et al. (2005) also implicitly acknowledge that the source of a better data fit comes from the *general* properties of a mathematical procedure, but not due to solely phylogenetic approach. The say, "Why the large difference in results? With a conventional analysis, each of the five data points is weighted equally for both computing the regression line and the prediction interval, and the place of the datum to be predicted (the desert ringtail's metabolic rate) is not considered in the sense that a star phylogeny (e.g. Figs 3A, 4A) is assumed, mathematically speaking. In the phylogenetic approach, two differences occur. First, the data points are weighted differentially when the regression line is computed, so it differs somewhat from the conventional line. Second, for computing the prediction interval, the algebra specifically recognizes that the desert ringtail population has a very close relative, the mesic ringtail population, which has a fairly high metabolic rate, and thus the prediction is 'pulled' to a higher value." One should only add for clarity that for the positively correlated values, which is always the case in phylogenetic analysis regardless of the considered traits, the weighing coefficients will be such that the data fit will be better, and the confidence interval can be manipulated. Thus, the authors' conviction that "This sends a strong message that we should routinely consider phylogenetic information in statistical analyses of comparative data." is a

consequence of mathematical interplay, the inherent property of the *mathematical procedure*, which will do the same things for *any* data, but not the effect achieved exclusively due to the use of phylogenetic information.

High variability of allometric exponents discovered by Garland et al. (2005) through 'phylogenetic correction', does not speak in favor of phylogenetic approach too: "It should be noted that the identity of the sister clade of passerines is controversial, and the foregoing example may well change as improved phylogenetic information becomes available.", Actually, such change for the considered mathematical methods will occur regardless if the new information true or false; even worse is the fact that there is no way to verify both older and newer results.

Overall, if we compare the phylogenetic approach with the earlier discussed criteria 1-9 for developing models, we can see a drastic departure from these concepts, towards more speculative and unilateral vision of the problem, away from the richness of reality and multitude of (often interrelated) real factors, towards virtualization of the working space and, I am sorry to say, to *principal* unverifiability. Computer simulations should not substitute for the real world, when it is possible to draw data and information *directly* from the reality, which is the only ultimate reference, one should validate any findings against. Otherwise, the mounting abstraction layers very quickly detach us from the real world. Garland et al. (2005) say that "Fortunately, simulations can use arbitrarily complex models of character evolution, limited only by one's ability to write computer programs and imagination". Such a vision is rather an unfortunate acquisition, which makes any good neither to authors, nor to the problem of interspecific allometric scaling. It would be much more beneficial to share the view of Westoby et al. (1995): "No statistical procedure can substitute for serious thinking about alternative evolutionary scenarios and their credibility.", with the addition of computer simulations and detached from reality imagination.

By and large, neither validation nor disproof of results obtained by phylogenetic approach is possible; what is obtained, has to be taken for granted. However, there is a particular example where the absurdity of the result obtained by phylogenetic approach is rather obvious. In (Shestopaloff 2016a), a plausible explanation of the fundamental causes of interspecific allometric scaling has been proposed. One of the considerations used in this analysis is an *empirical fact* that the allometric exponent for the increase of speed in mammals with the increase of mass is 0.209. A Reviewer, without any doubts in the rightness of what he is doing, courteously recalculated this value using phylogenetic information, obtained the number of 0.15, and apparently wanted me to relocate into a phylogenetic virtual space and use this value instead of the *actual* 0.209. Such a "correction" makes *absolutely no sense* in the context of my study, because that would mean that the animals move with much slower, some virtual speeds, related to nobody knows what to. This single "correction" immediately destroyed all deductions and the whole model, while the use of real data produced a theoretical value of allometric exponent coinciding with experimental observations to the third digit. Addition of similar phylogenetic transformations for animals' limbs, skeleton masses, etc. would make things even worse.

So, the phylogenetic approach, indeed, on average provides better data fit and allows manipulating confidence intervals. However, (a) the procedure itself and the obtained results are *principally* unverifiable; (b) as the discussion showed, we should reassign the lion's share of this

credit to the general properties of mathematical procedures, which will do the same for other data, but not to the validity and value of phylogenetic information.

The main doubtful achievement of phylogenetic approach, by and large, is that it invalidated all results and hypotheses, obtained since the discovery of the effect, while arriving to a dead end, from which no way to solving the problem of interspecific allometric scaling can be found, since the variability of allometric exponents the phylogenetic approach obtains leaves no hope for finding any regularity. At the same time, this is a common sense that all natural phenomena are defined by hierarchy of real factors. Conventional studies convincingly showed that the metabolic rate depends on mass, while residual values can be explained by ecological factors. The set of such factors can be further explored, including phylogeny, but there is no doubt that there is a hierarchy of *real* factors and underlying mechanisms, defining interspecific allometric scaling. They are there! So, let us find these mechanisms, their hierarchy and interrelationships. The phylogenetic approach, on the contrary, suggests stopping here and reflecting on impossibility of solving the problem, which is a ridiculous attitude, especially given the fact that there are very plausible, very likely to be true, explanations of the main mechanisms underlying this phenomenon *already*, which are just ignored, very much due to the dominance of phylogenetic approach.

### **The role of ecological factors**

Westoby et al. (1995) presented thoughtful and convincing arguments with regard to methodological considerations, and McNab, in the earlier cited works, showed that the same effects are much better explained by ecological factors, than by a "phylogenetic signal" perceived by Capellini et al. (2010) and others. Capellini et al. (2010) also acknowledged large variations of phylogenetic signal. This is rather an indication of inherent flaws of the approach, than the real nature of the phenomenon, for which many reasons can be given.

The quotes below from (Westoby et al. 1995) present much more measurable, reasonable and more constructive attitude towards the problem.

"Our essential message, however, is that a PC ('phylogenetic correction') procedure is not in fact a 'correction', an adjustment to remove errors. Rather, it is a conceptual decision to give priority to one interpretation over another. Accordingly, it is an error to believe that PC is a methodology that must routinely be applied in all comparative analyses."

(Our arguments above entirely support this thought - there are no evidences of validity of phylogenetic approach other than a better data fit, which is the property of mathematical methods, but not of the phylogenetic methodology.)

"There is almost always very substantial overlap between the portion of variation correlated with ecology and the portion correlated with phylogeny."

Indeed, phylogenetic and ecological factors interrelate, since phylogenetic traits much originate under the influence of ecological factors, and are selected by them. Phylogenetic traits are very much the *consequences* of ecological factors, while the *ecological* factors are the causes - a fact the phylogenetic approach entirely ignores. The other consideration is this. By and large, phylogeny is an *ascertaining* of historic developments happened under the influence of ecological factors (we do not consider random mutations, but these are first of all ecological factors, which "test" the mutations too). This historical past might have some influence on the present, due to certain inertia of biological adaptation mechanisms, or when environmental

conditions *do not require* changes. And, of course, such historical influence always has *limited* and *varied* time period. So, what is only certain, is that there is a *complex interplay* between the past and the present, between the available traits, adaptation abilities of organisms, and ecological factors. Ignoring any of these inputs inevitably distorts the whole picture.

"Actually, the allocation of trait-variation under PC corresponds to one extreme of the possible attributions of variation among different correlates. The other extreme ... would be to attribute the maximum possible variation to ecological correlates, leaving attributable to phylogeny only whatever residual could not be related to present-day ecology."

"But in reality, dominant mode of evolution generates patterns of trait variation that are both correlated with phylogeny and also maintained by the selective forces of present-day ecology." (True, and the proofs are many. Such patterns can be claimed as a "phylogenetic signal", even if they do not include one.)

"Phylogeny and present-day ecology should be thought of as complementary interpretative accounts, not as mutually exclusive components of trait-variation".

(As we said in introduction, these are two sides of the same phenomenon, and so both have the right to be considered, if one wants to understand this phenomenon.)

"... the hypothetical machinery connecting past cause to present outcome is that intrinsic properties the lineage constrain change over time. PC gives logical priority to the hypothesis that such machinery exists, over the hypothesis that such selective forces in the present favour similar outcomes to those in the past. In reality, the credibility of phylogenetic constraint or phylogenetic inertia must depend very much on the trait and on the time-scales in question."

Works (Shestopaloff 2016a, 2016b) provide evidence that, indeed, there are evolutionary forces related to the entire food chains, which shape the metabolic rate of organisms. Interestingly enough that McNab (2010), also emphasizes this factor: "The correlation of mammalian size with geography and time reflects the impact of temperature, rainfall, and season on primary production, *as well as the necessity in the case of some species to share resources with competitors.*" (Italics is mine.)

"Variation categorized as correlated with family membership only might in reality reflect a relationship through an ecological variable not included in the dataset, just as variation categorized as correlated with an ecological variable might in reality reflect a relationship through a family-specific morphological trait."

(This could be a very useful reminder to the adherents of phylogenetic approach, obtaining "phylogenetic signals".)

Note that the author of this paper came to almost all of these conclusions *independently*, before starting the literature search, so that the reader can add him to the list of supporters of more measurable approach too.

Studies done by B. K. McNab further enforce such views. In (McNab 2005a) he says:

"The variation of body mass in 62 species of mammals belonging to the Order Carnivora accounts for 86.8% of the variation in their basal rates of metabolism. When four other factors, substrate, food habits, habitat, and latitude are combined with mass in the analysis, the 98.7% of the total variation in basal metabolic rate is accounted for."

"That is, nearly all living organisms are a mosaic of characteristics that reflects both their past and present. The extent to which these characteristics of living organisms reflect these two factors, present circumstances and ancestry, is controversial."

"The basal rate of metabolism in the Order Carnivora is clearly influenced by many factors and they are complexly intertwined with each other."

"If these habits continue through time, the adjustments associated with these habits are continued, if the adjustments permit survival. The recent tendency to ascribe such adjustments to phylogeny ... is meaningless, except as it is a statement that the adjustments represent a commitment to particular habits. Besides, an allocation of residual variation to phylogeny prevents a detailed examination of the interaction among the factors associated with basal rate, which is fundamental to our understanding of the functional basis of ecology, behavior, and evolution. The possibility that basal rate of metabolism can be maintained independent of all external and internal requirements, as dictated by phylogeny, i. e., history, is unbelievable. Such a character is too central to daily life to permit it to be frozen by history and tolerated in a changing environment without a detrimental and ultimately fatal impact on species."

"The basal rate of metabolism in carnivorans, actually, is determined by principally by their body mass, food habits, climate, latitude, and substrate, and therefore is subject to change as these factors change."

Work (McNab 2005b) acknowledges:

"Some observers have argued that the principal factor influencing the residual variation in BMR is "phylogeny". Phylogeny then acts as a "collective" for the various interactive factors other than body mass that influence BMR."

"However, body mass accounted for 98.8 % of the variation in total BMR in 46 marsupials".

"Another potential approach, phylogenetic contrasts, preferentially describes most (or all) of the residual variation in a character state to "phylogeny," thereby ignoring the interaction of character states (McNab 2003b). As noted, "phylogeny" at best acts as a collective for the various factors influencing the residual variation in character states. In fact, most relatives are physiologically similar because they have similar habits and live in similar environments, a condition seen in arvicolid rodents (McNab 1992), but when a radical ecological or behavioral diversification occurs in a clade, as in the family Phyllostomidae (McNab 2003b), it is associated with a diversification in physiology, which is what is to be expected."

In (McNab 2006) one can find diligent reflections on the relationships of phylogenetic and ecological factors.

"Difficulties have been associated with its use (Westoby *et al.* 1995), the greatest of which is the autocorrelation of character states with phylogeny. This correlation, coupled with the decision in 'contrasts' to give preference to phylogeny as the explicative factor for the residual variation in a performance character, reduces the possibility that statistical evidence of its correlation with the environment and behavior can be demonstrated. The use of 'contrasts' may be acceptable when dealing with morphological characters, like the type of mammalian reproduction, if they contain an anatomical fingerprint of historical modifications that facilitate performance, but it is unsatisfactory for the performance itself."

"Performance characters are best examined in the context of the environment in which a species lives and with the other characteristics that the species has because the survival of species require that performances are compatible with conditions in the environment because its

resources are used to facilitate performances. Nevertheless, the evolution of performance character states from those of a species' ancestors should be examined to determine whether these states have repeatedly evolved and if so, whether they have the same consequences. But to imply that history is the only, or even the most important, factor dictating these performance states is misleading."

Work (McNab 2009) provides more supportive facts and considerations that these are rather ecological factors, which play the primary role in formation of organismal properties.

"The basal rate of metabolism (BMR) in 533 species of birds, when examined with ANCOVA, principally correlates with body mass, most of the residual variation correlating with food habits, climate, habitat, a volant or flightless condition, use or not of torpor, and a highland or lowland distribution."

"However, if physiological rates are considered, then it may not make any difference whether they were attained by ancestry or convergence because they must be in sufficient harmony with conditions in the environment and the species' behavior to permit the survival of species having these character states, at least as long as the function does not depend on a unique morphological structure. "

"Phylogeny influences the evolution of character states as a result of commitments made to solve problems previously encountered, sometimes restricting future possibilities and sometimes opening new opportunities, but they do not normally influence directly the narrow adjustments in physiology that connect behavior to conditions in the environment. That is, phylogeny may indicate whether a clade could evolve a particular food habit, but if that food habit evolves, energy expenditure reflects it and the environment in which the species lives."

"Besides, the most adamant supporters of phylogenetic analyses of physiological character states admit the direct impact of body mass on energy expenditure. My view is that some factors other than mass have the same effect, including at least food habits and climate".

The last three quotations explain, why one can and rather should consider *real data* and primary, *leading* factors, especially when it comes to functional traits, like metabolism, but not the *virtualized* data, obtained through phylogenetic trees or other transformation, representing the *past*. We should study the *real* world, the *real* animals, their *real* properties, which happened to be such at *this* moment. It is *this* balance between their abilities and demands of the environment, which matters the most. Maybe some past adaptations still have lagging influence, but the degree of this influence depends on many factors of different intensity and action time.

It is a "sufficient harmony" with the environment, which eventually selects such features, but not their mere historical presence. It is not only within each taxonomic rank that the adaptation occurs, but each organism adapts to the surrounding environment, and not rarely such adaptation changes are significant ones. So, the influence of historic developments should be evaluated extremely cautiously. Such influence, just due to the much higher priority of *present* needs over the *past* events, should not be significant, and especially in case of integral features, like metabolic rate. (Otherwise, what do the adaptation mechanisms exist for?) This means accordingly that the real data are of much greater informative value and reliability than the ones virtualized on the basis of the past, and especially when such a virtualization is presented as the only possible choice, and the past is considered as the only meaningful factor.

The work of proponents of phylogenetic approach (White et al. 2013) also confirms that the metabolic rate is not a permanent fixture (which it would have to be, if defined by historical development only), but noticeably changes in the *present* time: "The finding that metabolic rate is repeatable, but that repeatability declines with time, has implications for studies that test for phenotypic associations between metabolic rate and other traits", which is a clear evidence that phylogenetic information is not the only one influencing organismal metabolism. Also, the authors note that "most studies have found that metabolic rate shows low to moderate heritability". In other words, the metabolic rate is a parameter that does not depend much on previous developments, but is rather defined by the present needs within shorter time intervals. In case of individual organisms, life cycle's phases also are of influence. These facts lead to a conclusion that the validity of phylogenetic approach requires further studies, and its dominance as the only legitimate paradigm is very much questionable.

The work (McNab 2010) provides more insights into the complex interrelationships of different factors, affecting the allometric scaling.

"As always with correlations, one can never be sure that they unambiguously define their functional bases. The decrease in size and rate of metabolism associated with entrance into a desert might be related to some factor other than primary production, such as a depression of metabolism in relation to high ambient temperatures, or possibly in relation to balancing a water budget."

"...species become larger or smaller depending on the size, abundance, and availability of resources, which suggests that this integrated pattern could be called the "resource rule."

"The suggestion (McNab 1971) that body size in some carnivores varied with the presence or absence of larger competitors was most clearly illustrated in the puma and jaguar, the competitive explanation for which now has support."

The presented opinions and obtained results clearly show that this reasonable and measurable approach, supported by B. K. McNab, Westoby et al. (1995), Weibel and Hoppeler (2005) and many others, produces much more convincing and meaningful results. It does not ignore phylogeny as one of the possible factors affecting allometric scaling, but uses an integral approach, in which different factors can contribute to the phenomenon. In this regard, it is very different from a unilateral "phylogenetic" paradigm.

## Conclusion

The author need to pinpoint to the fact that phylogenetic methods, for a long time already, did not produce results, which would allow solving the problem of interspecific allometric scaling. On the other hand, more conventional studies propose very plausible explanations, supported by solid experimental evidences, and expose the fundamental causes of interspecific metabolic allometric scaling.

So, what should be done in order to move forward and eventually to solve the problem (or maybe recognizing already available solutions)? It is obvious that the monopoly and dictate of phylogenetic approach should be abandoned, and publishing results of studies, which do not use phylogenetic information, should not be considered as heresy. Such works should be given a serious meritocratic treatment on the basis of obtained results and presented proofs of their

validity, but not judging them by adherence to certain fashionable but speculative concepts and belonging or not to dominating "schools of thought".

The presented considerations showed that these are first of all mathematical interplays themselves, but not so much the phylogeny, which provide a better data fit, although even the better data fit by no means can be considered as evidence of truthfulness of the phylogenetic approach; for that, a conceptually solid scientific verification has to be provided, which was not done, and, actually, hardly can be done in case of phylogenetic approach.

The "phylogenetic signal", another working horse of phylogenetic method, is very likely can be the consequence of action of other factors, and of ecological factors especially, working in the same direction, as the quoted studies done by B. K. McNab and by others show.

Phylogenetic approach does not reject natural selection and evolution as such in principle, for which diversity of traits of individual organisms is obviously required. However, then, judging by their works, they focus on developmental history and separate, abstract their studies from the *sources* of this divergence, considering it as a thing existing in itself, independently of anything else. In fact, this is a very important, even critical, issue, which, once taken into account properly, would prevent many present "phylogenetic" oversights. Organisms have many adaptation mechanisms and means of transferring acquired features to their offspring (still much debated on different aspects issue, but nobody will deny that acquired features can be inherited). These adaptation abilities and the transfer of newly acquired features to offspring work at different organizational levels and different time horizons, helping organisms to adjust - *at different scale levels* - to the environments they live in. This is not a question that the highest priority of organisms is addressing the needs of the *present*, using all means available in their disposition. Organisms will change according to the demands of the environment, on the available basis, all the time adding to this base, and thus creating a new one for the next step. Similar thoughts were expressed by Westoby et al. (1995) and B. K. McNab. This undeniable fact of influence of the present means that the *physiological* adaptation is much tied to the *present* (represented by ecological factors) but not so much to the past, and that the influence of the present and the very recent past constitutes substantial, and often the *main* part of organismal properties. So, the action of these factors has to be accounted, for one thing, and it has to be accounted by their *real* values; not through unrelated to their nature corrections.

The adherents of phylogenetic approach exercise rather mechanistic view of the problem. Their approach is as follows: data are somehow dependent through the past, and so this dependence has to be removed or corrected. In this, however, they disregard other influencing factors, their different intensity, the presence of different mechanisms acting at different time horizons and scale levels, but foremost they disregard the *current* nature of the phenomenon, and that the mechanisms and caused by them adaptations, which are closer to the current time, *have to be* the most influential, and the more it is so, the more survival chances an organism has.

What is the whole issue about? An experimenter measures metabolic rates of different organisms (or other traits for that sake) and wants to find out, what factors caused the regularity of the rates' change, if any. One can just say that the past is the cause, which is what phylogenetic approach assumes. Then, the next question immediately arises - what was the cause of that past? Obviously, the past of that past, with such an approach. And so on, until we necessarily come to the First Origin. However, it is clear that all past events, in practical terms, always have a *limited* interval of influence, after which they can be neglected.

On the other hand, if we include into consideration ecological factors, then we will obtain a very logical, clear and transparent explanation of evolutionary changes occurring under the influence of different factors, while phylogeny would represent a *formal account* of these changes, a *report* of what was happening with regard to organisms' traits. This is what phylogeny is about - *ascertaining* the past, while the primary forces are adaptation mechanisms, working for the present under the stimulus provided by ecological factors. *This* real vision should be the base for the studies of interspecific allometric scaling. Such studies should preserve continuity with the previous conventional approaches, in that sense that they should consider *real* experimental data, subjected to taxonomical considerations, depending on the problem and data, and use normalizations and other data adjustments *extremely cautiously*, if at all. (It is so easy to destroy information, and especially its fine structure.)

Examples of such works producing excellent, advancing the discipline, results are many, like a very useful for my studies work (Weibel and Hoppeler 2005). The aforementioned studies (White and Seymour 2005; White et al. 2006) were very helpful too. This is a great pity that these authors *denounced* their *the best* scientific achievements in favor of fashionable and, as the presented evidences show, highly speculative unsupported phylogenetic paradigm.

The solution of the problem of allometric scaling assumes the need to know not only which factors influence, but also the hierarchy of these factors, their interrelationships, and *why* and *how* they influence. Dependence of metabolic rate on mass is the most important issue for this problem, of which all agree. Once we know the underlying mechanism of this dependence, we could add other factors to it. Such a methodological approach was used for unicellular (Shestopaloff 2016b) and multicellular (Shestopaloff 2016a) organisms, and produced revealing and encouraging results. The last study addresses the fundamental causes of the main, backbone relationship of the metabolic rate with mass, and describes particular components, together defining this phenomenon. They are as follows.

- (a) Scaling of limb masses (tails for fish);
- (b) Distribution of inertial masses between moving limbs;
- (c) Scaling of limb lengths;
- (d) Scaling of skeleton masses;
- (e) Scaling of the maximal metabolic power;
- (f) Fractions of the maximal metabolic power corresponding to basal and other specific metabolic rates.

The work provided simple transparent mathematical formulas how to combine these factors, in order to obtain the total allometric exponent. Other factors, in particular ecological ones proposed and studied by B. K. McNab and other researchers, then can be incorporated into this backbone model. Such studies, for the reasons discussed above, should use *real data*. Even if there is some data interdependency, it will affect the results significantly less than unverifiable phylogenetic corrections (this was convincingly demonstrated by application of phylogenetic corrections in the last twenty years), while conventional methods using *real* data produced lots of valuable results - nobody could deny this. The important implication of such an objective approach will be returning due respect to the whole body of previous works on allometric

scaling, whose value was significantly diminished, and in many instances even nullified, by the demands of adherents of phylogenetic approach that the only valid data to be considered from now on should be "phylogenetically informed" - an unsupported and flawed claim, as it has been shown in this article. On this updated basis, which will again include all previous conventional studies done almost for a century now, the discovery of fundamental level mechanisms of interspecific allometric scaling will promptly move forward, since so much is done already for its successful solution by previous generations (including the discovery of the effect itself, by the way).

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