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Morphological Disparity: An Attempt to Widen and to Formalize the Concept

Igor Ya. Pavlinov
Zoological Museum, Moscow Lomonosov State University,
Russia

1. Introduction

One of the key paradigms in the contemporary biology, now emerging, is based on the acknowledging diversity of organisms (aka *biodiversity*) as a fundamental property of the life. This property is immanent to the evolving biota and constitutes a special research domain with its own problematics, tasks and, in part, methods. *Diatropics*, a discipline dealing largely with specific properties and regularities of the diversity, was suggested to recognize not so far ago (Chaikovski, 1990). This conceptual framework serves as a kind of alternative to the classical physicalist paradigm having been absolutely predominating until recently which purports to reveal unified laws and so concentrates on the uniformity rather than on the diversity. From this physicalist standpoint, the diversity, if it falls out of certain overall trends, is treated as a kind of "noise" just preventing to reveal the uniformity expressed by those laws. The currently prevaailing concept of biodiversity was initially advanced to reflect its taxonomic aspect, more particular the species diversity (Norton, 1986). However, more recent development of this concept has led to understanding that the taxonomic aspect is far from adequate representation of the entire natural phenomenon called *the* biodiversity. Scientists working on diversity of organisms became to realize that taxa do not exist without their morphological (or any other) traits, that is, without those morphological (or any other) features that emerge in the evolution together with the taxa and constitute an essential part of the entire biodiversity. This yields renaissance of understanding of the latter as largely a diversity of morphological forms (Gould, 1989). And, consequently, the so called *morphological diversity* became recognized as one of the key aspects of the overall biodiversity deserving special attention and investigation. And this "dual" view of biodiversity was eventually fixed terminologically; its taxonomic aspect is now called *diversity* proper (multiplicity) while its morphological aspect merits the special term *disparity* (heterogeneity) (Erwin, 2007; Foote, 1996; Kaplan, 2004; Pavlinov, 2008; Wills, 2001). Investigations of this second aspect of biodiversity now draw much attention of both evolutionists and ecologists (Chakrabarty, 2005; Ciampaglio et al., 2001; Erwin, 2007; Faleev et al., 2003; Foote, 1993, 1996, 1997; Gerber et al., 2008; Hulsey & Wainwright, 2002; Mcclain et al., 2004; Kaplan, 2004; Roy & Foot, 1997; Wainwright 2007; Willis et al., 2005).

Notwithstanding that, morphological disparity (aka *morphodisparity*) still remains basically "tied" to the taxonomic aspect of the overall diversity; as a matter of fact, it is actually being studied as essentially a morphological dissimilarity among taxa (Foote, 1993, 1996, 1997; Kaplan, 2004; Roy & Foote, 1997). That is why it is infrequently still declared that it is the

taxonomy that deals with biodiversity. As a result, morphological dissimilarities among many other kinds of biological groups, such as sex or age groups, casts of social insects, biomorphs, etc, appeared not covered by currently predominating understanding of the disparity. However, it is evident that these dissimilarities constitute a very significant portion of the latter and hence they are to be given no less attention than the differences among taxa (Pavlinov, 2008).

This means that the very notion of disparity delimited by taxic differences only is quite insufficient. Instead, disparity is to be understood as a *compound of the dissimilarities among all and any kinds of biological groups of organisms* and not only among taxa. Accordingly, analyses of these dissimilarities in their plenitude should constitute one of the principal tasks of investigations on disparity as a whole. This disparity is morphological one as far as morphological traits are involved, but there are also other trait-defined disparities such as ecological, physiological, ethological, etc.

In the present chapter, I shall analyze some fundamental issues concerning morphodisparity in the above outlined widened sense. I shall start with consideration of background models underlying that understanding (section 2). It will be followed by discourses on the objectives of morphodisparity investigations (section 3), a part of which is causal interaction between disparity forms (section 4). Thereafter, some key parameters and characteristics of morphodisparity will be overviewed and formalized (section 5). Some attention will be paid to operationalization of those formalisms by means of numerical techniques allowing analysis of respective parameters (section 6), and several examples will be given to illustrate their application to particular datasets (section 7). At last, I shall consider briefly several important problems concerning general properties of morphological disparity to be considered more closely in future studies (section 8).

2. The background models

Any conceptual construct exists and functions not by itself but within a certain wider scientific framework, or background knowledge. It is this framework that provides the general understanding of what that construct specifically is, why are there different ways of its treatment and how it is to be dealt with (described etc.). Therefore it seems to me quite reasonable to start our consideration of morphodisparity matters with a very short reference to rather metaphysical topic.

The ways biodiversity can be understood and defined are different. This leads to several general concepts of biodiversity which underlay different understanding of what is the morphodisparity (Pavlinov, 2008).

The simplest is the *organismal* concept according to which only organisms are observable entities and thus are to be laid down in any definition of biodiversity. Theoretically, it is based on acknowledging the organism as a focal point of the life; accordingly, the biota is an array of organisms and the diversity is an array of organismal dissimilarities. Such a position is deeply rooted in the classical biology of the 18–19th centuries and is now largely supported by the Evo–Devo concept (see Hall, 1998 on the latter). However, this standpoint seems to be insufficient in respect to the entire biodiversity problematics. Indeed, such a reductional treatment looks no more biologically sound than, say, understanding of the organism as just an array of its cells.

The neo-Darwinian evolutionary theory presumes that the biota is structured basically at the population and species level. This gives a *species* concept of biodiversity (Claridge et al.,

1997), which is popular among environmental protection experts for it is quite operational and makes it easy to measure the taxic diversity (e.g. Sarkar, 2002). Accordingly to this standpoint, differences among species and their populations constitute the core of the biodiversity (and hence morphodisparity) isuue.

More general is the concept of biodiversity which considers this phenomenon at the biotic level. In its rather simplified version developed basically within phylogenetic taxonomic framework, biodiversity is treated as an array of dissimilarities among monophyletic taxa of any rank, that is, dissimilarities within the phylogenetic pattern (Eldredge & Cracraft, 1980; Pavlinov, 2005). Its further development led to acknowledging two other types of supra-organismal living systems as equivalent components of biodiversity, namely ecosystems (Faith, 2003) and biomorphs (Krivolutsky, 1998; Pavlinov, 2007).

Such a *biotic* concept of biodiversity, as it was further developed, fits quite naturally the modern consideration of biota from the synergetic standpoint (Pavlinov, 2007). According to a general model elaborated by this approach, development of such type of systems implies their structuring, that is, the emergence of certain subsystems (groups) within them recognizable by their specific features (Barantsev, 2003). This process of structuring is brought to existence and controlled by an array of causes, each responsible for producing groups of certain kind. Historical causes produce phylogenetic pattern of monophyletic groups while ecological causes are responsible for many other biodiversity phenomena, beginning from the differentiation of coenoses and biomorphs and going down to various infraspecific groups such as sexes etc. At last, there are intrinsic causes of development of organisms that are responsible for differences between ontogenetic stages and, hence, for existence of morphologically (physiologically etc) different age groups in populations. It is to be stressed that none of these general causes can be classified as more or less "important" in structuring biota; instead, they are equivalent in a sense, which makes biodiversity forms equivalent, in the same sense, as components of the overall biota's structure generated by different causes (but see about "primary" and "secondary" forms in the section 4 below).

The most significant consequence of such causal treatment of biodiversity as a biotic phenomenon is that it presumes a causal relation between biota's development, its structure, and forms (manifestations) of its diversity (Pavlinov, 2007, 2008). According to this, the biota is non-accidentally structured into various groups, be they either taxa, or sex or age or other infraspecic groups, or biomorphs, etc., each taking certain place in the biotic total structure and having certain peculiar features. So, it is the entire pool of various kinds of the disparity forms that constitutes the biodiversity as a whole. As it was just stated, this idea presumes that all such forms are, in the above sense, equivalent to each other.

3. What is the aim of the morphological disparity analyses?

According to the above biotic concept of biodiversity, the latter could be considered as a kind of *macroparameter* of the biota allowing to characterize it as a whole, regardless of its particular elements described by respective microparameters (pairwise differences among particular organisms and groups thereof). It reflects the very fact that biota is differentiated into certain groups of organisms produced by certain causes. These groups are dissimilar in certain features, the entire array of these dissimilarities is registered and studied as *the* morphodisparity.

It is evident that the latter does not exist by *per se*; rather, it represents a kind of epiphenomenon of the biota structured into groups dissimilar by morphological (and any

other) features. Thus, descriptors of morphodisparity also constitute an array of macroparameters of the biota allowing to characterize, explore and eventually explain certain aspects of its structure.

The latter makes quite obvious the answer to the question placed in the title of the present section. We study morphodisparity in order, before all, to reveal the structure of biodiversity manifested in the dissimilarities among various groups of organisms. As this structure is non-accidental relative to the structure of biota proper, the next level of generalization based on the analyses of morphodisparity will be about the biota's structure (pattern). And as the latter is non-accidental relative to the causes affecting the structuring process, the *ultimate goal of investigations of the morphodisparity is understanding of the array of causes structuring the biota* as the evolving and functioning whole.

Taking into consideration possible causes structuring the biota (historical, ecological, etc), several general approaches to the disparity analyses can be recognized (Pavlinov, 2008).

The first of them can be called the *structural* approach, which deals with the disparity structure as such, with its general properties, parameters and characteristics, with its basic elements and their interrelations, etc. Though just a "descriptive", it is the most fundamental approach underlying all others; it is evident that any causal consideration of the morphodisparity and then of the entire biodiversity is impossible without reconstruction of the disparity structure. The latter, as an object of investigation, is most usually being reduced to several particular forms subjected to a particular causal explanation, be it phylogenetic or ecological or other. Such a reductionism is presumed by limitations of paticular exploratory themes and so is unavoidable, but nevertheless the totality of the overall disparity structure is not to be forgotten. It is this structural approach that constitutes the main subject of the present chapter.

The next is the *adaptational* approach; it considers various forms of differentiation (and of disparity) as the results of particular adaptations to particular environments. Divergence between sexes within species with prominent sexual dimorphism, or between ontogenetic stages in insects with complete metamorphosis, or at last balanced polymorphism in populations – all of them could be treated as a reflection of the niche structure of respective natural communities. It is evident that this approach deals basically with ecological causes structuring the biota and making its diversity as it is.

Another approach can be baptized as the *evolutionary*; it eventually intends to reveal and understand evolutionary, or more precisely, historical causes of the biota's differentiation. It is this approach that serves as a framework for analysis of the above phylogenetic pattern in general and of morphological differences among monophyletic taxa (such as phylospecies) in particular.

At last, there is one more approach to the causal morphodisparity analysis worthwhile being recognized; it could be called the *ontogenetic* (or more strictly epigenetic). It considers mainly those dissimilarities which are produced by individual growth processes and explains interrelations between disparity forms in terms of the "growth factor" itself (Eble, 1999; Pavlinov, 2008). It occurs to me that, because the ontogeny itself cannot be interpreted directly in terms of historical or ecological causation, this approach cannot be reduced to the others just considered. However, the Evo–Devo concept is to be mentioned here as the one that might connect phylo- and ontogenetic approaches to the morphodisparity analyses.

Ontogenetic approach to understanding and analyzing morphodisparity is especially important in case of variation of the measurable traits. It is evident that, for the growing organisms, it is the ontogenesis that produces most of their differences at phenotypic level.

These differences may involve rate or/and duration of growth processes but the final result (other things being equal) will be the same: in some individuals the respective structure will be smaller in size than in others. Accordingly, morphological differences of such kind could be explained by growth pattern specific to respective groups of organisms, say, to the sex groups (Blackith, 1965; Mina & Klevezal, 1976).

4. A "succession" between disparity forms

Systemic understanding of the morphodisparity proper presumes implicitly some specific interactions between disparity forms, which are not isolated from each other. Such an interaction can be thought about as a kind of causal relation between these forms in a way that some of them might be, at least in part, causes of others. So the disparity forms could themselves be included in the system of causal relations defining the morphodisparity structure. The entire system of such causation between disparity forms can be designated as their *succession*. Accordingly, it is possible to classify disparity forms involved in such a causal interaction as "*primary*" and "*secondary*" ones, which means that certain portion of the latter is a consequence of the former (Pavlinov, 2008; Pavlinov et al., 1993, 2008).

In more explicit form, variation of measurable traits may serve as a particular case of such kind of interrelation between disparity forms. Accordingly to the above ontogenetic standpoint (see section 3), all differences between growing organisms by such traits could be explained in term of their linear growth. It makes age variation a kind of "primary" disparity form, just because variation of such traits is basically regulated by the growth process by definition. Correspondingly, other disparity forms can be thought about as "secondary" ones relative to the age variation; they are "superimposed" over the differences attributable to age variation while they emerge due to action of some other factors not reduced to the growth (say, sex or geographic ones).

Such an approach makes it possible to elaborate a kind of causal *null model* connecting various forms of disparity of measurable traits with the growth process (Pavlinov, 2008; Pavlinov et al., 2008). It differs principally from the one elaborated in respect to phylogenetic interpretation of the morphospace occupation (Pie & Weitz, 2005). The above so called "growth" null-model presumes that, other factors structuring the disparity not in effect, one has to anticipate some strong positive correlation between age and other disparity forms (sex, geographic, etc.) of the measurable traits involved in the growth process. Significant deviation from such a correlation means non-fulfillment of the condition implied by this null model and indicate a possible significant effect of other cause(s) irreducible to the "growth factor".

The same ranking principle could be applied to other disparity forms which could be interconnected by the "primary–secondary" relation. Positive correlation among individual and geographic variation constituting the so called "Kluge–Kerfoot phenomenon" (Kluge & Kerfoot, 1973; Mitton, 1997) seems to be another important case of such relation. Here, individual variation is the "primary" form and geographic variation is the "secondary" one; the latter could be considered as an "extrapolation" of the former over the territory (Sokal, 1976). (Note that I here do not concern possible mathematical aspects of this phenomenon considered by Rohlf et al., 1983.)

A concept of the "succession" relation between the disparity forms can also be applied to correspondence of within- and between-species differentiation of closely related species. The focal point here is that the original Darwinian concept of gradual speciation must mean, in the terms adopted here, high "succession" between subspecies and species differentiation

(Pavlinov, 2008; Pavlinov et al., 1993). This presumption may serve as another null model relevant to this kind of comparisons, according to which any significant deviation from it might indicate irrelevance of the Darwinian concept.

5. Basic notions

One of the most fundamental problems concerning morphodisparity is that the latter, if it is not reduced down to just a sum of dissimilarities among individuals but treated as a macroparameter of the biotic structure (see section 2 above), is not a directly observable matter. To the contrary, it is given to a researcher not as a such but only in the concepts, notions and estimates defined by the very researcher. This means that a sufficient thesaurus is needed in order to designate and to describe properly both the disparity itself, its forms and interrelations among them.

The most inclusive is notion of **disparity**, which designates *any and all manifestations of both dis- and similarities among organisms* by any kind of traits; as far as the latter are morphological, the disparity is also designated as the morphological one. Let any fixed aspect of the disparity be designated as a **disparity form** (or a *form of variation*); each disparity form could be considered as a **component** of morphodisparity. Any group of organisms homogenous in respect to all the disparity forms will be called *elementary*; respectively, the disparity observed within such elementary group corresponds by definition to the *individual variation*. Elementary groups arranged according to certain biologically meaningful variable defining certain disparity form (sex, age, species belonging etc) constitute a *composite group*; respectively, dissimilarities observed between the groups so arranged represent the *group variation* of the same name.

In modern researches of disparity, the latter is formalized by notion of **morphospace** (Eble, 2000; McGhee, 1991, 1999; Pavlinov, 2008; Stone, 1997). It can be defined as an *array of actual and potential states of a morphological system realized in an array of organisms*. With some reservation, it is equivalent operationally to the phenetic hyperspace (Eble, 2000; Sneath & Sokal, 1973).

Before going ahead with considering morphospace parameters and characteristics, it is worthwhile to stress especially that the morphospace is not identical to the morphodisparity proper. The latter, as it is here understood, is what does exist in the objective world, just because the organisms themselves and their features by which they are dissimilar are all objective (real). Unlike this, a morphospace does not exist without a researcher who defines it on the basis of respective notions, definitions and estimates by characters selected in some or other way, so it is largely subjective. One can think about morphospace as a kind of *model* of the disparity; it is used as a representation of the real disparity in certain operational form to which certain analytical methods and estimates could be applied properly. It is to be clearly understood, as well, that the morphospace is formed exclusively by morphological variables selected to characterize disparity within a particular group of organisms, so no "external" (physical) variables are taken into consideration when morphospace properties are analyzed. It is this "abstract" status of morphospace that allows to compare directly such different disparity forms as age, sex, and geographic variation regardless of their orderliness in the real (physical) world. It is evident that morphospace concept is analogous in some respects to the ecological niche concept, as the latter is based on analysis of certain ecological variables which do not actually exist out of certain formalized model of real ecological communities (Pianka, 2000; Vorobeichik, 1993).

Variables, by which morphological entities under comparison are described, define *axes* of the morphospace. This makes possible a geometric representation of the latter as a hypervolume. A unit observation corresponds to the morphospace *element* and is represented by a point in respective hypervolume. Position of each element in the latter is uniquely defined by a combination of variable states peculiar to it. Particular interpretation of both morphospace axes and elements depends on the morphospace consideration aspect, which can be twofold (Pavlinov, 2008).

Using terminology developed by numerical taxonomy (Sneath & Sokal, 1973), they could be denoted as *Q-* and *R-aspects*. In the case of morphodisparity, the *Q*-aspect corresponds to consideration of disparity forms in the hyperspace defined by the traits describing the morphological entities (individuals, morphotypes, etc.). Alternatively, the *R*-aspect corresponds to the consideration of the traits in the hyperspace defined by variables designating the disparity forms. As it is seen, the principal difference between them involves interpretations of morphospace axes and elements (points in the hypervolume). In the *Q*-considered morphospace, the axes correspond to original variables (traits), by which the objects under comparison (individuals, morphotypes, etc.) are described, these objects being morphospace elements. By this, the *Q*-considered morphospace is fully analogous to the standard phenetic hyperspace, positions of elements in which are defined by their respective traits states. Contrary to this, *R*-aspect provides a kind of *inverse* morphospace, which axes correspond to the variables designating disparity forms (sex, age, etc) and morphospace elements are not individuals (morphotypes, etc.) but their traits. Operationaly, the axes of *R*-considered morphospace are defined by some quantitative measure of disparity form, for instance by a portion of the total moprhodisparity attributed to this disparity form; respectively, positions of elements (traits) in moprhospace are defined by respective estimates of explained variance for these traits. Morphodisparity is rarely considered in such a manner, but it provides some interesting possibilities (see section 7 below).

In the geometric terms, components of morphodisparity can be identified as *subspaces* of respective overall morphospace. A strict correspondence between the above groups of organisms and their disparities, both elementary and composite, and respective subspaces in the given morphospace are to be postulated for the sake of operationality. Thus the entire morphospace is defined as consisting of elementary and composite subspaces corresponding to dissimilarities both within and among elementary and composite groups (Pavlinov, 2008; Pavlinov & Nanova, 2009). For two morphospaces, in one of which between-group dissimilarities are more prominent than in other, while within-group dissimilarities are the same, the total volume estimates in the Foot's approach will also be the same, which seems to be quite erroneous. This makes it clear that between-group interaction within a morphospace constitute quite important portion of the latter and cannot be ignored, so accentuation of this morphospace fraction in an explicit form is quite necessary. It is evident from this viewpoint that definition of morphospace as just a sum of (in the terms adopted here) its elementary subspaces (Foote, 1993, 1996, 1997; Zelditch et al., 2004) provides oversimplified morphospace concept.

The morphospace may be *empirical*, if it is defined by the observed data only, or *theoretical*, if at least some of its components are hypothetical or imaginary (Eble, 2000; McGhee, 1999, 2007); the latter can also be defined as a "space of logical possibilities" (Zavarzin, 1974). The theoretical morphospace may be *interpolated*, if the imaginary data fit strongly between the observed ones, or *extrapolated*, if the imaginary data exceed the boundaries defined by the observed data.

Analysis of correspondences between empirical and theoretical morphospaces is an important part of morphodisparity researches. It allows to reveal actually existing ("permitted") and non-existing ("forbidden") states of a morphological system under investigation, which is a significant task for some branches of theoretical morphology (Levinton, 1988; McGee 1999, 2007). It is to be noticed that such an analysis provides a kind of "bridge" between classical morphology dealing with organisms and exploration of diversity of these organisms.

If morphospace is defined by the original traits it can also be called *original*; if the traits are transformed some way, this gives *transformed* morphospace. An example of the latter is the hyperspace defined by principal components extracted from the original traits.

Morphospaces construing for the same dataset may differ not only due to consideration aspects or trait transformations but also because of use of different dissimilarity measures. For instance, Euclidean and correlation distances reveal different aspects of overall dissimilarity pattern (Sneath & Sokal, 1973) and thus structure the morphospace in different ways. Particular morphospaces thus obtained can hardly be classified as original or transformed; rather, they correspond to different *patterns* of the same morphodisparity. From such a standpoint, it looks incorrect to state (Foote, 1997) that a morphospace can be characterized by some general pattern regardless of metrics applied.

The most important and most general parameter of the morphospace is its **structure** defined as a relation between its elements and/or its subspaces (Pavlinov, 2008). Indeed, nearly any actual morphospace (even if it is delimited by individual variation) is structured; there are "clouds" of elements within morphospace and "gaps" among them which are caused by both evolutionary and natural history of organisms under investigation. It is clear that the structure refers, in most general sense, to differentiation of some group of organisms; the more it is differentiated, the more structured is its morphospace. In more restrictive sense, the structuredness reflects if there are any conspicuous subspaces within the morphospace studied and how distinct they are. The morphospace structure is quite multifold and includes several characteristics.

If the group variation is considered, the structure is characterized by morphospace *composition*, that is simply by a list of the disparity forms (composite subspaces) recognized. An important structural characteristic of the subspace is its *portion* in the entire morphospace; it is defined as a part of the latter occupied by respective subspace. Though being a characteristic of the structure parameter, it depends evidently on the volume estimates (see below).

Quite important characteristic of morphospace structure is the subspaces *overlap*. It could be defined most simply as a balance between within- and intergroup dissimilarities; a more sophisticated might be its definition by interrelation of partial subspaces within total morphospace (Pavlinov, 2008; Pavlinov & Nanova, 2009). Additional to overlap is the *hiatus* (gap) between (usually elementary) subspaces. These two characteristics, overlaps and gaps, yield a complete description of interrelations between subspaces within the given morphospace. This is one of the most "problematic" characteristics of the morphospace; it is similar in a sense to that known in ecology as the niche overlap (Pianka, 2000; Sohn, 2001; Vorobeichik, 1993) and so faces the same troubles.

Another characteristic of the morphospace structure is morphospace *occupation* which means unevenness of distribution of points within hyperspace (Ciampaglio et al., 2001; Erwin, 2007; McGhee, 1999). It is usually illustrated by some schemes showing either distribution of elements within a hypervolume (e.g. standard scatter-diagram) or certain

trajectories connecting these elements to indicate probable transitions between them, which corresponds in most advanced versions to so called epigenetic landscape (McGhee, 1999, 2007; Shishkin, 1988). If subspaces are recognized, this characteristic can more formally be defined through combination of all overlaps and hiatuses.

Particular descriptors and characteristics of morphospace and its subspaces can reasonably be identified as *scalar* and *vector* ones. Informally speaking, scalar parameters provide "static" descriptions, while vector ones provide "dynamic" descriptions of morphodisparity. One of the most general scalar descriptors of the *Q*-considered morphospace is its **dimensionality** understood in topological sense as number of axes defining the morphospace. This descriptor can be estimated in two ways. The *complete* dimensionality is defined by all variables (traits) that are used in the given study; it corresponds to the *complete* morphospace, where completeness is understood not in any "absolute" sense but in respect to the given trait set only. The *sufficient* dimensionality is defined by a number of variables which are selected from the initial set and are considered as sufficient, by some criteria, for adequate representation of morphospace as a disparity model. This smaller set of variables defines a subspace of complete morphospace, which could be called *reduced* morphospace. Certain correspondence exists between morphospace structure and dimensionality; the more structured is morphospace in some or other respect (other things being equal), the less is its sufficient dimensionality (Zelditch et al., 2004). So the morphospace dimensionality can be interpreted and used as an indirect measure of its structuredness.

The morphospace/subspace **volume** is one of the most general and informative scalar descriptors indicating a magnitude of disparity observed for the given set of individuals described by the given set of traits. The entire morphospace is characterized by *total* volume, its subspaces are characterized by respective *partial* volumes (Pavlinov & Nanova, 2009; Zelditch et al., 2004). The *absolute* volume is defined as a total sum of dissimilarities among the objects; geometric interpretation of morphospace allows to assess absolute volume as a sum of pairwise distances between points within respective hypervolume.

For the morphospace containing several subspaces, estimates of its total volume depend on interrelations (overlaps and hiatuses) between its subspaces corresponding to disparity forms. The morphospace total volume is equal to the sum of partial volumes only if the latter do not overlap and have no evident hiatuses; this corresponds to the above morphospace definition by Foot (1993, 1996). If there are overlaps of the subspaces, then the total morphospace volume is less than the sum of partial volumes of its subspaces. If there are hiatuses, the total morphospace volume exceeds the sum of partial volumes of its subspaces. An estimate of partial volume attributed to all possible combinations of overlaps and hiatuses may provide a kind of measure of overall morphospace occupation. It reflects to some degree, just as the morphospace dimensionality does, the morphospace structuredness: the greater this summary partial volume, the less uncertain (unexplained) variation, the more structured (by definition) the morphospace.

A particular value of absolute volume calculated for a particular dataset depends on amount of objects and traits and on dimensions of the latter. Due to this, estimates calculated for morphospaces defined for different datasets may not be compatible directly. To remove this effect, several corrected estimates of morphospace volume are introduced (Ciampaglio et al., 2001; Pavlinov & Nanova, 2009; Villier & Eble 2004; Wills 2001; Zelditch et al., 2004). One of them is a *relative* volume calculated to exclude effect of traits number and dimension, another is a *unite* (or specific) volume calculated to exclude effect of number of objects.

It is evident that any estimates obtained for these volumes inherently depend on particular definitions and numerical methods applied. Attention is to be drawn to an important difference in formal properties between various volume estimates as they are defined here. Absolute estimates for the entire morphospace and all of its subspaces are by definition (and calculation methods) strictly additive; one can say that the total absolute volume is "decomposed" into respective partial volumes without residue (Foot, 1993, 1996). The same is true for the relative volume estimates. Unlike this, the unit volume estimates are not additive: the arithmetic sum of partial unit volumes is greater than the total unit volume (Pavlinov & Nanova, 2009). This is because each partial unit volume is estimated as some "mean" value for an object (similarly to the deviate in dispersion analysis), and the total unit volume is roughly equal to an average of all partial unit volumes, some of which can be smaller and others can be larger than this average value.

Vector descriptors of morphospace allow characterizing both directions of predominating variation trends within each of the subspaces and their co-directionality. Vector representation of morphodisparity is not so popular as the scalar ones, although both its basic ideas and principles of analysis, at least in case of measurable traits, are quite simple and transparent for understanding (Blackith, 1965; Lissovsky & Pavlinov, 2008).

As a matter of fact, each disparity form involves certain differences between organisms or groups thereof by certain traits. With the morphospace defined by these traits as axes, these differences are represented as distribution of morphospace elements along those axes in accordance to the observed differences. It is obviously possible to fix a predominating trend for such a distribution (this is a routine procedure in many numerical ordination techniques) and to define it as a vector characterized by an angle relative to the fixed morphospace axes. If several disparity forms are analyzed at once, it is possible to compare them by this vector characteristic, that is, to explore co-directionality of trends of respective disparity forms in the given morphospace. The more similar are trend directions of disparity forms being compared, the less is the angle between respective vectors. It is clear that nothing like directions in the "physical" space is presumed by such a vector analysis; only abstract morphospace axes and vectors are considered. Similar approach is quite popular in researches in ecology and biogeography where various angular (correlation) measures of similarity are employed (Pesenko, 1982; Pianka, 2000; Sneath & Sokal, 1973).

Such a comparison of vectors can be conducted between both the same disparity form in various organismal groups and between various disparity forms within each of such groups (Pavlinov & Nanova, 2009). Say, one may wish to compare trends of sex differences in various species, or trends of sex and age differences in the same species. Operational interpretation of results of such comparisons in respect to causes of the similarity in question is quite simple: high co-directionality of trends means that the same traits are mostly involved in the disparity form(s) under comparison. However, more general (and more speculative) explanations for between- and within-species comparisons are different; high co-directionality might be interpreted as reflection of the above "succession" among disparity forms in some cases, while its interpretation as a kind of "parallelelism" would be more appropriate in others.

There is a restriction in these comparisons; they seem to be permissible only for the morphospaces defined by the same variables. By this, analysis of vector parameters differs markedly from that of the scalar ones. It is quite normal to compare, say, unit volumes of different morphospaces, one of which is defined by cranial and another by dental traits. But

comparison of such morphospaces by vector parameter seems to be unsound both biologically and operationally, and there seems to be no methods for analyzing co-directionality of, say, sex differences in the morphospaces defined by different traits.

All the above considerations are relevant to the *Q*-aspect of morphospace consideration which is much developed in this respect. As to the consideration of morphospace in its *R*-aspect, it is not so intensively studied and thus its properties are not so evident. Some scalar characteristics of disparity forms are most easy to use in this case, and their interpretations are most clear (Pavlinov et al., 2008). First instance of such a consideration of *R*-aspect of morphodisparity that gave certain important results is the above Kluge–Kerfoot phenomenon, which concerns concordance between individual and geographic variation of a set of morphometric traits. Subsequently, similar approach was extended to comparison of several forms of group variation (Nanova & Pavlinov, 2009; Pavlinov et al., 1993, 2008).

In the *R*-considered morphospace, it is possible to compare various disparity forms in the same group of organisms or the same disparity form in various groups. It is based on scalar characteristics, but the tasks it deals with are quite similar to those accomplished by the above vector parameter. The basic idea (Nanova & Pavlinov, 2009; Pavlinov et al., 2008) is that the axes of *R*-considered morphospace may be interpreted as the vectors corresponding to certain trends of the disparity forms. Respectively, distribution of traits in such inverse *R*-considered morphospace indicates degree of concordance of these vectors: the closer the points of hypervolume are disposed to diagonal of the quartile between the axes, the more concordant are respective trends of the given set of traits.

Thus, we have two approaches to exploration of co-directionality of trends in the morphospace, one of which involves vector parameter of *Q*-considered morphospace and another works with scalar parameter of *R*-considered morphospace. They yield quite similar results, but yet there is an important difference; it is possible to analyze the traits individually in the *R*-considered morphospace only, this option being unavailable in the *Q*-considered morphospace. Such a possibility is of evident biological importance; to realize it, one has to abandon an idea of the traits set as a kind of statistical ensemble on which certain simple regularities (like the above Kluge–Kerfoot phenomenon) are to be fulfilled. The latter idea belongs to a physicalist standpoint according to which only such regularities are of scientific importance while deviations from them are non-significant. As it was stressed at the beginning of the present paper, a standpoint like this is not productive in the explorations of the morphodisparity. As far as the morphospace is defined by not randomly but reasonably selected traits, there is no biological reason in opposing statistically significant "regularities" and irrelevant "deviations" from them. Instead, equal attention is to be paid to all and any manifestations of overall disparity pattern "tied" to particular traits or subsets thereof, as they may equally be biologically sound and deserve causal analysis (Pavlinov, 2008; Pavlinov et al., 2008).

6. Operationalization

As it was stressed above, the morphospace "exists" in form of notions, definitions and estimates; it is the latter that make the entire theoretical construct operational and concrete.

There is a great diversity of approaches and methods of quantifying morphospace parameters and characteristics, beginning with quite simple indices of differentiation and finishing with sophisticated statistic measures of overall disparity and its particular properties. Here I consider certain methodological problems and then outline briefly some

numerical techniques employed in my and my colleagues' investigations, which are based on the above morphospace parameters and descriptors.

First of all, it is to be stressed that numerical methods employed in exploration of the morphodisparity should and could not be independent of biologically sound premises underlying this concept. The latter is the biological one, so the methods of its investigation are to be biologically reasonable; this means they are to be at least compatible with those premises and at most deducible from them. A spectacular example of such interrelation between theoretical and methodical parts of a research program in biodiversity studies is provided by cladistics in which techniques of construing branching diagrams are directly deduced from a particular phylogenetic theory (Pavlinov, 2005).

Another quite evident requirement for the methods of analysis of morphospace parameters is that they have to be transparent in respect to their formal properties. Therefore, these methods are to have pretty good mathematical background and are easy to understand and interpret by biologists not experienced in mathematics. Without this it is hard to hope for a clear-cut understanding of the results obtained by these methods. However, it does not mean that such a criterion would overbalance the one of biological validity, as it is sometimes suggested (Abbott et al., 1985).

At last, it is important that the methods in question should provide commensurable numerical estimates of various disparity forms, be it individual variation, sex or age differences, etc. It is evident prerequisite for various disparity forms to be directly comparable by their quantitative characteristics.

Let us consider briefly some methods which allow numerical analyzes of morphospace parameters introduced in the previous section and satisfy just above properties.

The morphospace sufficient dimensionality is usually assessed by some ordination methods such as principal component analysis (PCA) or multidimensional scaling (MDS) (Faleev et al., 2003; Puzachenko, 2000; Zelditch et al., 2004). The main difference between these two is that PCA operates on covariation/correlation matrices while MDS operates on distance matrices and thus is free from some limitations inherent to correlation analysis. There are several possible ways to assess numerically this parameter. In the most simple case, it is conventionally defined as certain portion (for instance, 75 per cent) of the disparity studied which is "explained" by respective number of variables; this number is taken as a value of the sufficient dimensionality. More sophisticated is an approach based on analysis of distribution of stress values obtained by sequential iterations of MDS procedure. The serious limitation inherited in these methods is that they do not allow to discriminate various disparity forms and to compare them by sufficient dimensionalities of respective composite subspaces. Such a possibility could be provided by Variance Component Analysis (VCA) or Discriminant Function Analysis (DFA), both applied to a priory recognized subgroups corresponding to the disparity forms. It is to be noticed that numerical values of sufficient dimensionality obtained by any of these approaches can be both integer and fractional numbers. The latter might be of special interest, as it allows to reflect also supposed fractal properties of the entire morphospace and its subspaces.

The total morphospace volume and partial volumes of its subspaces are currently being analyzed by various dispersion-based or distance-based methods (Eble, 2000; Faleev et al., 2003; Foote, 1996, 1997; Van Valen, 1974; Villier & Eble, 2004; Zelditch et al., 2004). The main (but not principal) difference is that dispersion-based methods imply *a priory* decomposition of the entire sample dispersion into within- and between-group dispersions, while distance-based methods are free of such precondition, which provides some specific merits (see

below). Both approaches allow analyzing (using the terminology adopted here) total and partial volumes, though they treat relation between these estimates in different ways. In the dispersion-based methods, the primary goal is the analysis of composite subspaces formed by between-group variation, while within-group variation is treated as just an unexplained variance which is not analyzed at all. In distance-based methods, either only elementary subspaces are initially analyzed or both elementary and composite subspaces are considered as equivalent components of the entire morphospace deserving equal attention. It is important that, within each of these approaches, all disparity forms are estimated in the same units and thus are comparable directly.

The nowadays most popular dispersion-based methods are the Multivariate Analysis of Variance (MANOVA) and the above VCA. The descriptors of disparity forms are considered by these methods as independent variables and morphological (and eventually any other) traits are considered as dependent variables. In MANOVA, the independent variables are uniformly taken as fixed, while VCA treats them as random. The both conditions seem to be too strong for the disparity forms actually involved in the biological investigations, so this provides certain problems (Leamy, 1983; Pavlinov, 2008). As a matter of fact, there are disparity forms, such as geographic or age variation, in which particular values (geographic localities or age groups) are actually non-fixed though hardly completely random, while other forms such as sex differences are certainly fixed. This inconsistency could conventionally be resolved by taking all the disparity forms as non-fixed independent variables in the dispersion analysis (Pavlinov et al., 2008).

Among algorithms of this analysis, Models I and III of both MANOVA and VCA, and maximum likelihood models of the latter are the most used (Ciampaglio et al., 2001; Leamy, 1983; Pavlinov et al., 1993, 2008; Zelditch et al., 2004). The Model I applied by Leamy (1983) seems to be least appropriate, as its dispersion estimates ascribed to particular independent variables are correlated significantly with the order they are entered in the analysis (StatSoft…, 2010). The maximum likelihood VCA was shown to be quite conservative in respect to variation of factor gradations and "sampling defects" producing more or less unbalanced design (Lissovsky & Pavlinov 2008). It could be applied as the prime method of *Q*-considered morphospace analysis while Model III of MANOVA is of use for the analysis of *R*-considered morphospace.

The subspaces overlap is impossible to explore directly by dispersion analysis, especially if overlap of the elementary subspaces is of interest. Meanwhile, it is principally possible to consider respective factor interaction as an indirect measure of composite subspaces overlap, but this question needs future special clarification (Pavlinov et al., 2008). Among dispersion-based approaches, standard DFA can also be employed here, in which disparity forms are again considered as classificatory (independent) variables and the traits are considered as dependent variables. Subspaces overlap could be estimated as per cent of posterior re-classification of objects allocated to the elementary groups recognized in respect to the given disparity form. This technique has been earlier employed in analysis of niche overlap (Krasnov & Shenbrot, 1998). Its results are quite easy to interpret, principal shortage of this method is that it does not allow considering the entire morphospace volume when overlap of its subspaces is evaluated.

Another approach to be considered here includes distance-based methods. Most usually they are based on calculations of Euclidean distance obeying the metric axioms, though correlation distances could also be used for some particular tasks (Sneath & Sokal, 1973). The first kind of distance makes the morphospace analysis faced at the problem of trait

dimensions, which is easy to resolve by introducing respective correction factor (briefly discussed above). Unlike the dispersion-based methods, number of elements in the morphospace matters in this case; thus dimensionality of distance matrix is to be included in the formulas used to estimate respective morphospace scalar characteristics. This approach makes it possible to analyze both volumes of morphospace and its subspaces and their overlaps. Several techniques of calculations are in use (Ciampaglio et al., 2001; Foote, 1997; Pavlinov & Nanova, 2009; Villier & Eble, 2004; Zelditch et al., 2004).

In the most simple case (Foote, 1997; Zelditch et al., 2004), the distances among objects and a centroid are calculated for each elementary subspace separately to give an estimation of the latter's partial volume, and then the total morphospace volume is calculated as a sum of all the elementary ones (see notes on its insufficiency above). Another approach is based on calculation of distances among all elements and the centroid of the entire morphospace, after which volumes for both partial subspaces and the total morphospace can be calculated (Ciampaglio et al., 2001; Foote, 1997; Zelditch et al., 2004). This method is more advanced, as it includes both within- and between subspaces dissimilarities; its shortage includes impossibility to discriminate directly these two sets of dissimilarities and to analyze separately composite subspaces corresponding to the forms of group variation. In our approach (Pavlinov & Nanova, 2009), we calculate pairwise distances among all objects without detecting any centroids, and then the entire distance matrix is decomposed into several blocks each corresponding to the particular elementary and composite subspaces.

Three correction factors are to be taken into consideration in calculations of scalar characteristics of mophodisparity, which are (a) number of traits by which the objects are compared, (b) trait dimension related to the general problem of size/shape components in the analyses of measurable traits, and (c) the number of objects in the sample being analyzed. These factors are widely discussed in respective literature and so are to be just mentioned here. Numerical techniques for analyses of vector parameters of morphodisparity first offered by Blackith (1965) was based on the above DFA. The latter however provides just an indirect evaluation of both directions and co-directionality of the vectors. These characteristics can be obtained straightforwardly from MANOVA based on the original Pearson's (1901) idea: the predominating trend ascribed to the given disparity form is defined and calculated as the first eigenvector of covariance matrix for the factor effect corresponding to that disparity form (Lissovsky & Pavlinov, 2008; Nanova & Pavlinov, 2009). Accordingly, similarity of two trends is defined and calculated as a cosine or arccosine of the angle between two respective eigenvectors (Lissovsky & Pavlinov, 2008).

It is evident that this operational definition of vector parameter is true for composite morphospaces and cannot be applied directly to the elementary ones. However, it is in principle possible to apply this concept to the latter using, for instance, PCA operating with respective covariance matrices and extracting eigenvectors from them (Eble, 2000).

This vector estimate deals with *Q*-considered morphospace and is hardly applied to the *R*-considered one. For the latter, Pearson's correlation analysis could be applied to estimate numerically concordance between values of explained variances ascribed to the particular traits in respect to the disparity forms being compared (Pavlinov et al., 1993, 2008).

To make my brief review more complete, information statistic measures of diversity/ disparity are to be mentioned, which are popular among ecologists and are used sometimes in morphometrics (Faleev et al., 2003; Kupriyanova et al., 2003; Pavlinov, 1978; Pustovoit, 2006; Zelditch et al. 2004). As far as scalar characteristics of the morphospace are concerned,

principal disadvantage of these measures is that they evaluate only evenness of a trait frequency distribution and do not consider magnitude of its variation; so they do not allow measuring morphospace/subspace volumes.

Although all the above morphospace estimates are treated as strictly quantitative, the task of evaluation of their statistical significance can be of interest. Several null hypotheses (not to be mixed with the above null model) are formulated and tested to reach this aim. One of them concerns significance of differentiation of groups fixed in respect to a particular disparity form under consideration. This kind of null hypotheses is formulated as follows: a characteristic (volume, vector, etc) of the given disparity form does not differ from the one caused by random variation. Another kind of null hypotheses concerns differences between these disparity forms by some characteristic used in their analysis (volume, overlap, co-directionality, etc). In this case, a relevant null hypotheses looks like that: difference between two disparity forms by respective characteristic is accidental. Null hypotheses of the first kind are easy to test by standard methods in case of dispersion-based approaches. Thus, both volume and vector estimates for any composite subspace can be tested by *F*-criterion. However, this statistical procedure cannot be applied for testing the second kind of null hypotheses above; nor can it be used in case of the distance-based estimates at all.

There are several distance-based methods of morphospace/subspace comparisons by their respective characteristics. The most simple is comparison of the morphospace/subspace volumes, for which standard parametric *t*-test seems to be appropriate. It allows to evaluate statistical significance of differences between any pair of morphospaces/subspaces by their volume estimates (Zelditch et al., 2004). However, more popular is a non-parametric approach that employs various resampling methods (Pavlimov & Nanova, 2009; Villier & Eble, 2004; Zelditch et al., 2004). They imply bringing some stochastic component in the original data matrix and subsequent analyses of thus generated matrices by standard algorithms. Comparison of the morphospace characteristic estimates for the original data matrix with stochastically generated distributions allows to calculate a probability of non-randomness of the original estimates.

To sum up the present section, I should like to stress that any formalized analytical approach is much simpler than the disparity being analyzed, so the latter is to be reduced some way to an operational state accessible to that approach. There are no universal quantitative methods which would provide reasonable decisions of all the tasks of biologically sound morphodisparity explorations. Each method is more or less narrow in its resolutive abilities and uncovers just particular properties of the overall disparity. For instance, of the two dispersion-based general methods, dispersion analysis makes it possible to measure volumes of morphospace and its subspaces but does not allow analyzing overlap of the latter, while DFA yields simple (though not complete) estimate of subspaces' overlap but provides no straightforwardly interpreted estimates of their volumes. As to the distance-based methods, they seem to be universal, but have their own limitations inherited in diversity of distance measures which choice is not a trivial task. Therefore, there should be a kind of "toolkit" with several methods included in it that would make it possible a more a less comprehensive analysis of various morphospace parameters and characteristics.

At last, it is wise to keep in mind that there are no "good" or "bad" methods by themselves; they become so due to their proper or improper application. This again turns us to the fundamental problem of interrelation between biologically sound backgrounds and technical tools of the morphospace exploration. One has to interpret a method properly within the background framework to comprehend if it is reasonably "good" or not.

7. Some examples from mammal skull variation

Below I shall present briefly some results of my recent investigations of morphodisparity fulfilled on skull variation in several mammal species. The principal "model" species in question are the pine marten (*Martes martes*), the red fox (*Vulpes vulpes*), and the polar fox (*Alopex lagopus*); some examples are borrowed from the data on the jirds (genus *Meriones*) and on the Przewalskii horse (*Equus przewalskii*). The skull is described by 14 standard measurable traits taken by caliper (the character list is not of particular relevance here). Most of these results were published elsewhere, together with description of the materials and particular methods (Lissovsky & Pavlinov, 2008; Nanova & Pavlinov, 2009; Pavlinov et al., 2008; Pavlinov & Nanova 2009). I shall consider here the following results: sufficient morphospace dimensionality and volumes estimates; some scalar and vector characteristics of *Q*-considered morphospace; scalar characteristics of *R*-considered morphospace.

Sufficient morphospace dimensionality was estimated by PCA for no less than 75 per cent of explained variance. It was found that the respective estimate is between 2 and 3 in the pine marten and the red fox, it is between 3 and 4 in the polar fox, and is reachs about 6 in the Przewalskii horse. So it can be concluded from the promises underlying this approach that the entire morphospace is much less ordered in the latter species as compared to others.

Estimations of subspace volumes were considered using data for pine marten and polar fox by means of dispersion analysis. The pine marten was represented by one geographic sample, sex and age differences were analyzed, four age groups were recognized. The polar fox was represented by four geographic samples, which allowed to consider spatial differentiation; sex and age differences were also considered, with two age groups recognized. These two species were shown to differ markedly from each other by the summary subspace occupied by all forms of group variation; the latter takes about 74 per cent of the morphospace volume in the pine marten and about 42 per cent in the polar fox.

These two species differ from each other also by ratios of partial volumes of the subspaces corresponding to the sex and age differences. The first disparity form takes much greater portion of the entire morphospace as compared to the second one (67 and 5 per cent, respectively) in the pine marten, while they are more similar in this respect in the polar fox (11 and 21 per cent, respectively).

Results of distance-based analysis of subspaces obtained for pine marten and polar fox indicate that the entire morphospace unit volume is higher in the former than in the latter (0.310 and 0.235, respectively). So the marten is more variable in general than the fox (of course, by the skull traits and in the units used here). As far as elementary subspaces are concerned, males appeared to be more variable than females in both species in all age groups, average values are 0.212 and 0.182 in the pine marten and 0.212 and 0.208 in the polar fox, respectively.

Analysis of composite subspaces indicate that overlap of age groups is evidently more expressed as compared to that of sex groups in the pine marten (0.843 and 0.437, respectively), while these values are almost equal in the polar fox (0.693 and 0.662, respectively). These results agree with well-known estimates of age and sex differences in these two species obtained previously by traditional approaches.

Estimations of co-directionality of disparity forms have never been considered any seriously before, so the results obtained on the skull variation in the above mammal species are quite new. Two principal approaches to analysis of this parameter were adopted in my studies, one dealing with integral (for all traits) vector characteristic of *Q*-considered morphospace

and the other being based on scalar characteristic (partial volumes of respective subspaces per traits) of *R*-considered morphospace. Within-species disparity forms (geographic, age and sex variation) were considered in the carnivoran species, while subspecies structure of a polytypic species was compared with the differences between closely related species in the jird genus *Meriones*. The angles between respective vectors were measured by their arccosines (in rads), the lower arccosine value indicates less angle which thus means higher co-directionality.

Comparisons of vectors of age differences with those of sex and geographic differences within each of the carnivore species revealed the following. Co-directionality of age and sex variation was estimated as rather high in the canids (0.16–0.29 rad) and pretty low in the marten (0.75 rad). It is evident from these results that the two canid species are more similar to each other in respect to their age and sex variation than to the pine marten. Co-directionality of age and geographic variation was estimated as rather high in red fox (0.23 rad) and low in polar fox (0.72 rad).

Interpretation of this within-species vector comparisons presumes a kind of "succession" between disparity forms caused by the "growth factor". Thus, differences among males and females in canids by their skull dimensions may be interpreted as resulting basically from differences in rate/duration of their linear growth. To the contrary, sex differences in the pine marten cannot be explained in such a simple manner but involve noticeably different allometric trends. The same seems to be true for the comparison of age and geographic variation in the canids. In the red fox, cranial differences between animals from various geographic regions may be explained mainly by differences in their linear growth. Contrary to this, geographic differentiation in the polar fox cannot be explained by such simple regularity, differences in growth patterns are to be anticipated (Nanova, 2010).

Calculation of angles between vectors of particular disparity forms in the carnivores indicates that (*a*) predominating trends of sex differences appear to be quite similar in all species (0.11–0.28 rad), (*b*) those of age differences are more diverse (0.24–0.60 rad), and (*c*) the trends of differences between geographic samples in the morphospace are most different in two fox species compared (0.68 rad). It is of importance to note that canid species appeared again to be more similar to each other by the vector characteristics calculated for sex and age differences, than each of them to the mustelid.

The results of such between-species comparison were offered by me to interpret as reflections of a kind of "parallelism" of morphospace properties in various species (see Section 5 above). It might be reasonably supposed that such a "parallelism" is caused by similarities in mechanisms structuring these species' morphospaces. Thus, one may infer from the data just exposed that such a similarity in mechanisms regulating various disparity forms is most expressed in case of sex differences, less so in age differences, and the least so in geographic differences. These similarities and differences among species are possible to explain, at least at a very general speculative level, as a consequence of certain balance of intrinsic (developmental) and extrinsic (environmental) factors. From this standpoint, trajectories of sex differentiation by skull dimensions come out to be quite similar in all species compared because they are most dependent on just the intrinsic factors which seem to be quite stable by themselves. Contrary to this, drastic between-species differences in predominating geographic trends in the same morphospace could be explained by that they are mostly regulated by some extrinsic factors, which are quite variable and so their manifestations are quite different in the species under consideration.

Analysis of co-directionality of subspecies and interspecies differentiation by skull traits in several closely related jird species of the genus *Meriones* revealed quite unexpectedly opposite directionality of these two disparity forms, numerical estimate yielding negative correlation (about -0.59) between respective distributions of explained variances attributed to different traits. It is evident from this comparison that some traits vary between subspecies of *M. libycus* while others discriminate three close species (*M. libycus*, *M. shawi*, *M. grandis*). Based on the speculative suggestions underlying such kind of vector analysis (see section 4 above), it is possible to interpret this disparity pattern in *Meriones* as indirect indication of various traits being involved in subspeciation and speciation events, respectively. If this treatment is correct, then other than Darwinian speciation model could be in action in this particular case, for example the one supposed by punctuated equilibrium concept (Eldredge & Gould, 1972).

8. Some problems and tasks for the future

Investigations of differences among organisms have as a long history as the history of entire biology. However, the structural approach to the morphodisparity having been developed during the last decades seems to provide a new insight into this biological phenomenon. As a matter of fact, it means a new look at the disparity, namely a look at its own properties and eventually at the causes of these properties. In this respect, structural approach to the analysis of disparity of morphological objects may be of no less "revolutionary" significance to the morphometrics than geometric morphometric approach to description of these objects themselves (Rohlf & Marcus, 1993). In other words, the structural approach to the morphological disparity may constitute a basis of a new research program for the morphometrics.

This program is at the beginning of its elaboration and therefore contains a number of problematic positions concerning the very fundamentum of respective background theory. They are mostly biological rather than technical and so their decisions would appeal to a kind of "scientific metaphysics" of biodiversity (Pavlinov, 2007). Though metaphysical, discourses of this kind have actually a significant impact on operational definitions and, respectively, on the methods of analysis of morphological disparity. Some of these problems are briefly discussed here.

First of all, the very understanding of the central notion of morphospace is to be indicated. As I stressed above (see section 5), its comprehensive definition has to include subspaces corresponding to the dissimilarities both within- and between groups of organisms, which can either overlap or be separated by hiatuses. So the morphospace is to be defined operationally as a combination of all elementary subspaces minus subspaces of their overlaps plus subspaces of their hiatuses. It is evident that, generally speaking, any elementary subspace can overlap with some subspaces and be separated from others. This provides a rather complicated overall pattern of morphospace occupation which, nevertheless, is to be assessed by adequate numerical methods. Our efforts lead us to a pretty sophisticated index, which however appeared to allow to analyze only a narrow part of this occupation (Pavlinov & Nanova, 2009). It is evident that the entire problem deserves special investigations in the future.

Several other problems may be united under the same cover that might be called morphospace non-Euclidity (Pavlinov, 2008). The latter, in the particular case under consideration, means non-orthogonality of the morphospace axes, which means that angles

between them may vary along their gradients. Translating these into biological terms faces us at the well known problems of between-trait correlation and size-dependent allometry, the latter providing a kind of specific developmental "allometric subspaces" within the entire morphospace (Gerber et al., 2008). There is a number of well known formal technical decisions of these problems, for instance replace of correlated original traits by respective uncorrelated principal components. However, content-wise consideration of this subject inclines me to suspect that such kinds of decisions seem, at least in part, to deprive them of biological sense, as they eventually lead to a loss of quite important and biologically sound fraction of morphodisparity.

Between-traits correlations deserve special consideration in this respect. As a matter of fact, these correlations are formed by the same growth processes as the traits themselves. So it seems quite reasonable to treat this "growth correlations" as a significant aspect of the morphospace defined by measurable traits. Therefore their elimination from explorations of the entire morphospace would reduce biological contents of their results. Instead of formal elimination of correlations from analyses of a morphospace by, say, defining the latter by principal components, it would be more reasonable to find the proper ways of special investigations of impact of correlations onto morphospace properties. For instance, it might be promising to divide traits into certain blocks ("pleiads") accordingly to their correlations (Rostova, 2002) and to analyze each block separately to reveal specific properties of the subspaces defined by respective traits. The evident background of such kind of investigations includes a supposition that the stronger is correlation between traits, the more similar are the factors structuring their variation. So comparative structural analysis of morphospaces defined by various sets ("pleiads") of traits may serve as another important source of information about causal mechanisms of the overall morphospace patterning.

9. Conclusion

1. Morphodisparity is a macroparameter of the structured biota, the latter being understood as a developing complex non-equilibrium system. The overall disparity thus understood includes various disparity forms corresponding to dissimilarities among all and any kinds of groups of organisms as components of the structured biota.
2. The ultimate objective of analysis of morphodisparity is uncovering mechanisms (causes) effecting both process and results of the biota's development and structuring. This objective requests prior investigations of properties of the disparity proper, as they are defined by interrelations among disparity forms. Such a structural approach to the investigations of morphodisparity may constitute the conceptual core of a specific research program in the morphometrics.
3. The key notion in analyses of morphodisparity is that of morphospace. The morphospace differs from the disparity itself in that the latter is objective (real) while morphospace is a theoretical construct largely depending on definitions and descriptors (variables and methods) employed in the given investigation. Basic components of a morphospace are elementary and composite subspaces corresponding to the particular disparity forms.
4. Two consideration aspects can be fixed for morphospace analysis, Q- and R-aspects. The former corresponds to consideration of disparity forms in the hyperspace defined by the traits, while the latter corresponds to consideration of the traits in the hyperspace defined by the disparity form descriptors.

5. Morphospace can be characterized by scalar and vector parameters and respective quantitative characteristics. Scalar parameters include morphospace dimensionality, volume, subspaces overlap and distinctness, the latter two defining morphospace occupation. The overall morphospace volume is to be defined as a sum of volumes of elementary subspaces minus subspace(s) of their overlap plus subspace(s) of the hiatuses separating them. Vector parameters include directions of predominating trends of particular disparity forms and their co-directionality in the same morphospace.

6. As far as measurable traits are involved, a kind of null model of causal relation between disparity forms can be elaborated, which allows to classify at least some of these forms as "primary" and "secondary" ones. This model presumes that certain properties of the secondary forms are explained by properties of the primary ones. In such a case, it is possible to interpret relation between primary and secondary disparity forms as a kind of "succession" which can be strong or week. Particular contents of such null model depends on the background theoretical construction. For instance, for the diversity of growing organisms, age variation can be considered as a primary form relative to sex and geographic variation, which provides a simple "growth model" for explaining interrelations among such disparity forms. Another example of such null model is a pretty strong succession between subspecies and close species divergence presumed by the Darwinian microevolutionary model.

7. Serious restriction of the methods considered herein follows from their being linear and additive, while morphospace, in at least some of its properties, is non-linear and "non-Euclidean". The latter quite significant property means the morphospace axes non-orthogonality caused by correlations and allometric relations among morphological traits. This problem is to be considered as before all a biological and not just a "technical" one, because at least some between-traits relations are of biological nature and so are also the part of the overall morphodisparity.

10. Acknowledgements

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Research in Biodiversity - Models and Applications

Edited by Dr. Igor Pavlinov

The book covers several topics of biodiversity researches and uses, containing 17 chapters grouped into 5 sections. It begins with an interesting chapter considering the ways in which the very biodiversity could be thought about. Noteworthy is the chapter expounding pretty original "creativity theory of ecosystem". There are several chapters concerning models describing relation between ecological niches and diversity maintenance, the factors underlying avian species imperilment, and diversity turnover rate of a local beetle group. Of special importance is the chapter outlining a theoretical model for morphological disparity in its most widened treatment. Several chapters consider regional aspects of biodiversity in Europe, Asia, Central and South America, among them an approach for monitoring conservation of the regional tropical phytodiversity in India is of special importance. Of interest is also a chapter considering the history of the very idea of biodiversity emergence in ecological researches.

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