Morphological Modularity and Macroevolution:

Conceptual and Empirical Aspects

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INTRODUCTION

A notion of morphological modularity is often implicit in systematics and paleontology. Indeed, the perception of morphological modularity is manifested in the very existence of anatomy, comparative anatomy, and taxonomy as disciplines, and provides a rational basis for treating organic diversity as a combinatorial problem in development and evolution. In practice, it corresponds to the recognition that phenotypic wholes can be decomposed into parts, or characters. This basic analytic stance has been present to varying degrees throughout the history of biology, was particularly important in Darwin's and Mendel's work, and persists to this day (Darden 1992; Rieppel 2001).

Yet the parts and characters routinely identified by the morphologist reflect hypotheses of modularity based on observational or quantitative criteria, without reference to the generative mechanisms or the theoretical contexts to which modules relate. In contrast, a notion of developmental modularity has recently been explicitly advanced in terms of mechanisms of genetic and epigenetic specification of units of phenotypic evolution (Raff 1996; Wagner 1996; Wagner and Altenberg 1996; Bolker 2000). Because morphological patterns of organization emerge in ontogeny, morphological modularity might thus be seen as an aspect of developmental modularity. Accordingly, a research program emerges: the validation of putative morphological modules as developmental modules. This is of particular interest, as it could help further approximate evolutionary morphology (including systematics and paleontology) and evolutionary developmental biology.

A complementary research program presents itself, however, once modularity is seen as a property that is differentially expressed across hierarchical levels (Simon 1962; Bolker 2000; Raff 1996; Raff and Raff 2000; Raff and Sly 2000; Wagner 2001). Descriptively, mechanistically, and theoretically, modules at different levels may demand level-specific characterizations and may reveal phenomena unique to particular spatial and temporal scales. Descriptively, morphological modules are objects defined in terms of geometry, topology, and statistical considerations. A standard of discreteness is usually present, and the amount of information they encapsulate can often lead to rigorous characterizations. This information may be biased by taxonomic practice and the history of comparative anatomy, but reliable identification and justification of characters is possible beyond their use as a means to the distinction of taxa. Mechanistically, definitive morphological modules are established usually late in ontogeny, are subject to considerable epigenetic specification, and their variation will be mostly related to allometric growth. They define a unique, post-morphogenetic organizational level where module identity is maintained by morphostatic mechanisms partially decoupled from the developmental pathways of various module components (Wagner and Misof 1993; Wagner 1994). Morphological modules and modularity are thus a legitimate level of causal explanation and study, to which generative mechanisms relate necessarily, as a source of precursors, but not sufficiently. Theoretically, morphological modules have unique roles at the organismal level and above, participating causally in the structuring of ecological and genealogical systems in microevolution and macroevolution. They therefore stand as process-based natural kinds (Quine 1969; Boyd 1991; Wagner 1996,

2001). All in all, the recognition of a legitimate phenomenological domain for morphological

modules does not reduce the value of describing their microscopic structure, of expressing

them as instances of developmental modules and understanding their developmental origins,

or of treating them as causally inconsequential in some theoretical contexts. It simply

recuperates the ontological semi-independence of morphology, along with the entities and

processes it helps define. The complementary research program is then the characterization,

mechanistic interpretation, and theoretical articulation of morphological modularity <u>at</u> the

morphological level, but with explicit conceptualization of morphology as a multifactorial

phenomenon connected to multiple levels and multiple scales in development and evolution.

The advantage of the reification of morphological modularity is that it can be more

directly interpreted in terms of classification and systematization; it can be studied in fossil

groups and nonmodel organisms, thus allowing a broader window into the evolution of

modularity; and it can more readily allow exploration of macroevolutionary issues. The

challenge to evolutionary and developmental morphologists is to devise protocols of study of

morphological modules and modularity per se, and to develop intepretive schemes that are

consistent with but that at the same time enrich evolutionary theory. On the theoretical side,

theoretical morphology and theoretical morphospaces provide a way of directly modeling the

range of possibilities specified by particular modular organizations. This is not dealt with

here (see Rasskin-Gutman, this volume). Empirically, the proper study of morphological

modularity demands rigor in the description and representation of form, as well as consistent

criteria for the decomposition of wholes into parts and for the definition of classes of

autonomous behavior. This contribution addresses some key empirical aspects of

morphological modularity, including the identification of modules, the quantification of

modularity, and the relationship between modularity and macroevolution.

IDENTIFICATION OF MORPHOLOGICAL MODULES

Observing or inferring the existence of particular modules presupposes some

definition of what constitutes a module. Different definitions are possible depending on

which criteria are chosen, and on whether descriptive, mechanistic, or theoretical

individuation is sought. While a unified notion of module is highly desirable, it may not

always be useful in the morphological domain, because morphological units are complex

multidimensional geometrical objects whose identity, generation, and role may vary

differentially over scales of time and space and be often discordant. Still, a minimal notion

can help in highlighting similar assumptions and goals across research programs.

Minimally defined, morphological modules are cohesive units of organismal

integration. Module cohesion will usually arise from stronger interactions within than among

modules (see Simon 1962), and organismal integration will reflect differential interactions

among modules. This perspective leaves open the question of what constitutes "interactions",

which can for example be seen as structural relations (Riedl 1978; McShea and Venit 2001),

pleiotropic effects (Bonner 1988; Wagner 1996; Wagner and Altenberg 1996; Mezey et al.

2000), patterns of gene expression (Gilbert et al. 1996; Raff 1996; Raff and Sly 2000), or

function (Wagner and Schwenk 2000; McShea and Venit 2001; Schwenk 2001). This

minimal definition of morphological module is thus consistent with, but not equivalent to, general definitions of developmental module (e.g., Bolker 2000).

Within an organism or bodyplan considered in isolation, modules are *organizational* units. Among organisms, they are also *variational* units. Organizational morphological modules refer explicitly to the interactions postulated to be important in organismal construction or activity. They invite observation or description in terms of mechanistic relations, whether variation among organisms is present or not. As such, organizational modules are units of stability. Variational morphological modules reflect the strenghts of interactions and their potential disruption. They can be inferred from the variation and covariation patterns of descriptive units, which may or may not be modules themselves. There is no necessary one-to-one relation between particular organizational modules and particular variational modules, because the nonlinear mapping from genotype to phenotype, from part to whole, and from structure to function may affect organization and variation differently in time and space. Methodologically, a match or mismatch will also hinge on what counts as organization and as variation.

Organizational morphological modules

Different kinds of interaction justify different notions and partitionings of organization. (1) Structural relations characterize an organization as a set of geometrical objects, each of them spatially individuated by discrete boundaries or by shape differences, and thus standing as a module (or part -- see McShea and Venit 2001). (2) In terms of

pleiotropic interactions, the relevant organization is the genotype-phenotype map and modules

are clustered pleiotropic mappings (viewed as routes, not vehicles) that "align" genotypic and

phenotypic space (Wagner 1996; Wagner and Altenberg 1996). (3) Developmental

interactions have multiple material bases, and several types of organizational modules stem

from them, such as fields of gene expression (Gilbert et al. 1996), genetically mediated

spatiotemporal patterns of cell and tissue differentiation, proliferation and movement (Raff

1996), domains of epigenetic dynamics (Goodwin 1984; Webster and Goodwin 1996), and

regions with localized allometric growth. (4) Functional cooperation of parts, in turn, make

organization a matter of functional integration and performance, and modules the sets of

functionally individualized units (even if spatially distributed) underlying organismal survival

and reproduction (e.g., Wagner and Schwenk 2000; Schwenk 2001).

Clearly, substantial overlap must exist among these various kinds of interaction and

the modules they underlie, for logical and evolutionary reasons. It is also conceivable that

some of them are reducible to others (e.g., cell types to patterns of gene expression, function

to structure, pleiotropy to function), but chance, redundancy, and differences in

dimensionality render complete reduction unlikely and mismatches inevitable. This is of

fundamental interest in the dissection of hierarchies and multiple chains of causality.

Heuristically, valid organizational morphological modules can be variously identified as

structural units by an anatomist, as functional units by a functional morphologist, as

pleiotropic clusters by a quantitative geneticist, or as developmental units by a developmental

biologist. If module identification in each case is also couched on consistent methodological

criteria, if it is refutable, and if it allows modules to be units in theories of process (see

below), the choice of approach will be anything but arbitrary.

Of much interest, concomitantly, is the comparison of differently identified modules.

If there are mismatches, how substantial are they? Do they reflect a difference in

evolutionary history, in constraints, in ecological contexts, or in ontogenetic stages? Can they

sometimes be ascribed to chance or to inferential error? If there is some common

denominator for morphological modules, the comparative study of differently constructed

morphospaces (e.g., Lauder 1995, 1996; Eble 1998, 2002a) may yield unifying insights on the

multifariousness of organizational morphological modules and their representation.

Variational morphological modules

While organizational morphological modules are mechanistic units of stability,

variational morphological modules are units of actual or potential change. The notion of

character is central here, because most characters are identified primarily as units of variation

in related organisms (Fristrup 1992, 2001). More precisely, valid characters are routinely

perceived as units of *independent* variation (Darden 1992). Independence is operational, not

absolute, being equivalent to the notions of "quasi-independence" (Lewontin 1978) and "near-

decomposability" (Simon 1962). Further, the degree of inferred character independence may

depend on how variation itself is sampled and analyzed.

In many contexts, independent characters are inferred from the observation of

correlations among units of description and quantification (Olson and Miller 1958; Lewontin

2001). The units, such as morphometric variables, need not correspond to modules. Modules will correspond to different directions of variation, and to covariation clusters. In addition, the units considered may vary to any degree within and among species. Modules are implied by actual dissociability in collections of organisms treated as contemporaneous.

In contrast, the discrete morphological characters often used in phylogenetic analyses stand for stable units of evolutionary variation across species, assumed to be independent by virtue of corresponding to individual historical events and thus suggesting potential dissociability in evolutionary time. Character correlation or coevolution does not affect their status as separate entities.

These different notions of character independence codify different timescales and potentialities of variation. Variational morphological modules may therefore also be of different kinds, as with organizational morphological modules, but here the primary determinant is the dynamics of interactions among units and of actualization of instances of units, not the interactions themselves. Characters as variational units are not incompatible with them also being units of organization, when the partitioning of variation follows the « lines of least resistance » defined by differential organizational discreteness within the organism. But given various kinds of organization and of variation, the relationship between organizational modules and variational modules may not be straightforward. Making sense of this relationship is most relevant to further understanding of the nature of modularity, and it can originally inform analogous issues, such as homology and homoplasy, or more generally lineage stasis and change.

Morphological modules as causal actors

Beyond their organizational and variational properties, modules can also be construed as having causal roles. Morphological modules are then instances of process-based natural kinds, i.e., as units that play a role in a process or set of processes (Quine 1969; Boyd 1991, 1999; Wagner 1996, 2001; Webster and Goodwin 1996; Griffiths 1999). In this sense, the characterization of morphological modules presupposes the choice of a reference class of processes. Such processes may be for example developmental, as existing modules affect the ontogeny of other modules; physiological, as in homeostasis; ecological, such as predation or competition; or evolutionary, such as selection or speciation. Modules become entities endowed with theoretical significance, and their individuation a matter of identifying dispositional properties (propensities) determining their potential participation in the processes of interest (Wagner 2001). These properties are causally inert (as with fitness understood as a propensity -- Sober 1984). They reflect expected behaviour, not causes per se. The actual causes are to be found in the mechanisms of organization and variation.

A one-to-one correspondence between particular processes and particular causes is not a sine qua non, and therefore the identification of causal morphological modules is not reducible to the study of organizational and variational modules. Process-based individuation may seem only appropriate when a general theory is available, which may be the case for evolution but not for development (Bolker 2000), but causal roles can be consistently identified under any degree of generality, and can be usefully referred to even if the respective theories and postulated causes turn out to be inadequate. The identification of modules is a

heuristic endeavour -- process-based and pattern-based approaches are best seen as complementary.

QUANTIFICATION OF MORPHOLOGICAL MODULARITY

From the fact that modules can be identified observationally or inferentially, it follows that modularity is present. Its quantification, however, need not always demand making the modules explicit. Further, it is highly context-dependent. And given that modules can be organizational or variational, modularity can accordingly also be seen as a constitutional property of individual organisms (and its parts) or as a relational property of sets of organisms. Organizational modularity is the state-of-being modular. Variational modularity is the state-of-varying in modular fashion.

In some contexts, it may be of interest to treat modularity as a nominal, presence-absence feature on the scale of the whole organism or its parts. Indeed, for dynamic modules such as morphogenetic fields, or for the terra incognita of the genotype-phenotype map, assessing the presence of modularity is a major goal. Further, because modules may often have a nested arrangement, the issue of whether they are themselves composed of modules at a structurally similar level of organization arises. This is not a trivial issue because internal cohesion may be specified in different ways. For example, the tetrapod limb is usually considered a module, but is it composed of modules whose origin and maintenance can be referred to the same hierarchical level(s) of organization? This may depend on whether a morphogenetic or a structural approach is used. For whole organisms, modularity is bound to

be present at some level, and intuitively at more than one level, but it may not be ubiquitous or isomorphic across levels.

Organisms and their modules are modular to different degrees (Kim and Kim 2001). Given that we do not know how much modularity can vary, numerical assessments of discrete and continuous variation should be attempted whenever possible if we are to achieve a complete understanding of the evolution of modularity. Statistics for modularity are thus needed. Importantly, the comparative study of modularity justifies, and may at times require, the use of proxy data and testable working assumptions as strategies in research. Below is an outline of possible approaches.

Number of characters or parts as proxies for modularity

Discrete morphological characters are standard data in morphological research and may be the most amenable to quantitative analyses of the evolution of modularity. They are similar to what Mcshea and Venit (2001) called "parts": operational units of the construction of an organism, and which can be expected to be a representative sample of the "true" underlying units, to be defined mechanistically or by theoretical role. In general, most characters defined on consistent topological and geometrical grounds as discrete units will correspond to such modules by proxy – hypothetical when described but cohesive and bounded enough to justify a strong assumption of individuation *in some context* (e.g., developmental, functional, evolutionary). If made explicit, this assumption can be tested on other grounds. An arbitrary character is hardly a module; but a comprehensive list of

characters or parts that takes into account organismal integration (or disintegration) could be seen as a hypothetical list of modules. In practice, if error in characterizing morphological units as proxy modules is reasonably small or random, useful estimates of modularity can be produced and comparisons made (see McShea and Venit 2001).

Counting characters is not equivalent to counting modules, but large differences in numbers of characters at a similar organizational level are likely to be correspond to differences in number of modules. In well-circumscribed groups, counts of characters standing for modules by proxy are intuitively appropriate as measures of relative modularity. This will be especially true for groups studied by a single author or for which general consensus on morphological terminology exists.

Even so, the kind of module of interest may influence how many morphological units are counted. For example, in a study of bryozoans McShea and Venit (2001) provide a number of protocols for counting part types, assumed to be functional units. Repeated structures where excluded and treated as belonging to the same functional unit. If the focus is on structural or developmental organization, however, finer assessments of modularity may be possible, and repeated structures can provide useful data. This will often be the case for skeletal features, which allow greater taxonomic and temporal coverage. Sea urchins, for example, have skeletons composed almost entirely of calcite plates. Plate number and shape can vary substantially, but since they arise sequentially from standard locations in the apical system, they could be viewed as repetitions of the same type of module. On this scale, modularity is essentially uniform. But on other scales, variation in rate, timing, and location

of skeletal growth individuates additional types of module. In terms of numbers of plate columns, sea urchins are more modular in the Paleozoic than in the post-Paleozoic. In terms of regional plate differentiation, irregular sea urchins are more modular than regular sea urchins. At the limit, each plate is a module of localized and potentially dissociable growth with stronger internal integration, afforded by the continuity of stereom trabeculae, than external integration, mediated by collagen fibers at boundaries between plates. Thus, in terms of plate number, a sea urchin with 1000 plates is more modular than one with 100 plates. While a focus on a single aspect or scale is justifiable on theoretical grounds, consideration of multiple contexts provides a window into the scale-dependent manifestations of modularity.

Morphological integration

Counts of discrete parts or characters may provide good proxy estimates of modularity for many comparative studies, but they do not take into account the full extent of differential integration within and among modules. The quantification of changes in within- and among-module integration can also important in assessing the relative frequency of various mechanisms of module evolution, such as cooption or parcellation (Raff 1996; Wagner 1996; Wagner and Altenberg 1996). When modules are hypothesized a priori based on mechanistic criteria such as function or developmental identity (e.g., Mezey et al. 2000; Eble 2000; Klingenberg et al. 2001), patterns of morphological integration within and among sets of traits provide tests of the importance of postulated mechanisms. Alternatively, morphological modularity can be hypothesized a posteriori, from analysis of nested patterns

of physical association and of covariation among traits, and later validated on mechanistic grounds.

A focus on integration within modules is of interest not only as a distinct measure of modularity, but also when a complete inventory of parts or characters is not possible for preservation reasons, as happens with incompletely known fossil species, or when the theoretical focus is on particular modules. Mezey et al. (2000) devised a statistic for within-module integration: the ratio of the total number of module traits affected by a set of quantitative trait loci to the maximum number of traits that this set could affect. Higher than average integration is considered significant. The reference standard in assessing significance may be a randomized distribution of interactions within a population (see Mezey et al. 2000). A strictly morphological generalization of this statistic, and immediately applicable whenever gene effects on traits are not available, as will often be the case in systematic and paleontological studies, is to quantify trait interactions. The statistic then becomes the ratio of the total number of trait interactions within a module to the maximum possible number such traits could allow. What counts as a trait interaction can be either physical contiguity, in which case shapes and positions matter, or inferred sign of covariation, against a chosen standard (zero, average, random, etc.). The reference distribution of interactions may be based on individuals within populations, or on species within clades, if interspecific variation is being considered. Further, theoretical models of morphological transformation can provide an alternative to randomization as a basis for formulating null predictions, when the shape and local connectivity of morphological traits is available (e.g., Rasskin-Gutman 2003).

When the number of characters is small or constant, or when characters vary substantially in shape and connectivity, measures of morphological integration among putative modules will be most informative. The degree of integration among modules is inversely related to their parcellation. A statistic for parcellation was suggested by Mezey et al. (2000): a chi-square comparison of the observed vs. expected number of module traits affected by each quantitative trait loci. A morphological generalization of this statistic is also possible, measuring trait interactions among modules either in terms of neighbouring relations (e.g.,Rasskin-Gutman 2003) or of the sign of covariation.

The *strength* of covariation may vary substantially across morphological units, and can be used to produce more precise estimates of modularity. Morphometric approaches are readily applicable in this context. On morphometric grounds, wings as putative modules were confirmed in *Bombus empatiens* and *Drosophila melanogaster* (Klingenberg and Zaklan 2000; Klingenberg et al. 2001). Yet the greatest potential of morphometrics lies in the recasting of exploratory studies of morphological integration in terms of modularity. A number of studies have postulated and documented the existence of morphological covariation sets, reflected statistically in trait correlations and interpreted in terms of function, development, or other factors (Olson and Miller 1958; Zelditch et al. 1992; Zelditch and Fink 1996 ; Eble 2000, 2003). Covariation sets, viewed as putative variational modules, become important data for documenting the evolution of morphological modularity across the phylogenetic hierarchy.

Disparity

Disparity, the spread or spacing of forms in morphospace, is an aspect of biodiversity relating to phenotypic distinctness in a sample. It has become an important quantity in macroevolutionary studies (e.g., Gould 1989, 1991; Foote 1993, 1997; Wills et al. 1994; Wagner 1995; Eble 2000), and it holds promise in ecology (Roy and Foote 1997) and evolutionary developmental biology (Eble 2002a,b).

Disparity is a general measure of variation, and as such no assumptions are made about its causes. Yet it can often be decomposed or scaled into contributions likely to reflect variational modularity. Variational modularity relates to spatially and theoretically contextualized variation, and therefore stands as a major aspect of variability (the potential to vary – see Wagner and Altenberg 1996). Because modularity specifies opportunities for semi-independent variation, a correlation between extent of modularity (in terms of numbers of parts, within-module integration, and among-module integration) and extent of disparity should be found. Disparity is *not* formally equivalent to modularity, but for many problems in morphological evolution, trends in disparity can be a useful proxy for trends in variational modularity. This interpretation of disparity follows from the established use of patterns of natural variation as guides to the existence of constraint and differential variability (Alberch 1983, 1989; Shubin and Alberch 1986; Foote 1995, 1999; Wagner 1995; Wagner and Altenberg 1996; Eble 2000). The recognition of disparity as a large-scale aspect of modularity suggests new research directions in quantitative morphology and new perspectives for the interpretation of the causal role of disparity in macroevolution.

If morphological disparity is to be used to quantify morphological modularity, the nature of the assumed modularity-disparity connection should ideally be specified, to allow for additional tests. This may involve postulating what are the hypothetical modules, identifying developmental, functional, or other mechanisms thought to affect overall modularity and disparity in a similar way (e.g., mutation rates, developmental constraints, functional integration), or indicating common causal roles (e.g., in evolvability, in innovation production, in species and clade selection and sorting, in homoplastic evolution, etc.). Eble (2000) explored this connection in heart urchins, by focusing on a comparison of temporal disparity patterns between two sets of landmarks thought to reflect differential functional and developmental modularity. The connection was validated by the finding that disparity change and differentiation of the more integrated unit (set earlier in ontogeny) was more protracted over time, in contrast with the less integrated unit, in which most of the disparity is produced early in the history of the group.

Character or part counts, morphological integration, and disparity are statistical estimates of morphological modularity reflecting both organizational and variational aspects. As such, they encapsulate a variety of causes and roles for modules. Especially in macroevolution, causes and roles may change in importance across clades and time. Extensive quantification of patterns of morphological modularity will be needed if the preeminence of particular causes and roles is to be ultimately validated.

MORPHOLOGICAL MODULARITY AND MACROEVOLUTION

How does morphological modularity change in macroevolution? Can macroevolutionary phenomena significantly affect the temporal patterning of morphological modularity expected from microevolutionary theory? Is the impact of phylogenetic constraints on modularity potentially different in macroevolution? Addressing such issues will be needed to properly contextualize modularity in macroevolution. A step in this direction is to consider from an explicitly macroevolutionary perspective the relationship between modularity and various features of evolution, such as complexity, evolvability, innovation, stochasticity, and trends.

Complexity

Bonner (1988) suggested that as complexity increases, selection for localization of mutational effects would lead to increasing prevalence of gene network organization, in other words, modularity. Complexity, treated as number of cell types within organisms and as number of species in communities, was suggested to broadly correlate with size. It is unclear that complexity actually increases in evolution (Gould 1996; McShea 1996), but these suggestions lead to the expectation that modularity should correlate evolutionarily with number of cell types, with species diversity, and with size. Number of cell types can itself be seen as a measure of organismal modularity, although circularity is avoided if it is contrasted with morphological modularity at other levels of organization. A correlation between number of cell types and number of bodyplans is often reported (Kauffman 1993; Valentine et al.

1994). Recasting bodyplans in terms of disparity should allow a broader range of inferences to be made.

Species diversity could be seen primarily as an aspect of the "modularity" of ecological communities or of clades, but a connection with organismal modularity is also possible. The latter was investigated in a recent study (Yang 2001), which suggested that holometabolous insects have higher diversification rates than hemimetabolous insects because their more extensive metamorphosis specifies more modular juvenile and adult stages. How characteristic diversification rates might mechanistically relate to modules is a difficult issue, but if correlations can be consistently found across clades, modularity would stand as an important causal aspect of species and clade sorting and selection. Some macroevolutionary trends in modularity (see below) could therefore be documented and modeled in connection with long-term trends in species diversity through time.

A relationship between modularity and size follows from the connection between dissociability and allometry. Assessment of degree of allometry (Hughes 1990) provides a way of indirectly studying how size influences modularity. Large size may provide greater opportunities for morphological individuation, but as the shape of allometric trajectories will be the critical factor, exploration of the size spectrum may be more important in the macroevolution of modularity than maximization of size per se.

Evolvability and innovation

Wagner and Altenberg (1996) suggested that the modularity of the genotype-phenotype map determines evolvability. Evolvability was defined as "the genome's ability to produce adaptive variants when acted upon by the genetic system" (p.970), and also as "the ability of random variations to sometimes produce improvement" (p.967). This latter definition is immediately applicable to the morphological level. Yet by focusing on evolvability as adaptability, it remains most relevant to microevolutionary selection scenarios, given the expectation of adaptation to changing environments. In macroevolution, improvement may readily occur when morphological change is anagenetic, but will often be absent in cladogenesis, since speciation is nonadaptive with respect to species persistence. Major innovations and clade founding may also often not represent improvement because they usually correspond to discrete events decoupled from the adaptive context (the fitness landscape) of the parental clade. Because a notion of adaptive improvement is not always justified to contextualize interspecific variation and macroevolution, a further generalization of evolvability is possible: "the ability of variations to sometimes produce evolutionarily significant change". What counts as significant may differ depending on temporal scale, on hierarchical level, and on the degree of concordance between morphospace structure and fitness landscape structure. In studies of macroevolution, significant morphological change may be identified as an improvement in functional efficiency in some instances, but for operational reasons (the data of systematics and paleontology) and theoretical reasons (the centrality of novelty in macroevolution, regardless of the causes of sorting), significant

morphological change can usefully stand simply for "substantial distinction". In this way,

evolvability can be effectively quantified throughout the history of clades.

Variability is the potential to vary. Evolvability is the potential to vary in a relevant

way. Rate of positive mutation is a possible measure of evolvability at the molecular level.

Origination and innovation rate might analogously be used for morphological data. Disparity,

in turn, often measures variation only and is a proxy for modularity. However, the amount of

disparity produced relative to time or diversity is likely to reflect evolvability. Similarly, the

ratio of major morphological innovation to minor morphological innovation (Eble 1998,

1999) or the frequency of homoplasy (Wagner 2000) could be used. Another possibility,

appropriate for both modularity and evolvability, is to use measures of stationarity of

morphological variation through geological time (e.g. Foote 1995) or of cumulative change

through the history of clades.

Modularity as a by-product of stochastic morphological evolution

In stochastic simulations of the evolution of independent morphological characters,

Raup and Gould (1974) found that statistically significant pairwise character correlation is

common. They interpret this as the result of stochastic lineage sorting of character

combinations of clade founders, and of the progressively smaller probability of return to

average original states as dimensionality increases (which is a property of random walks). In

stark contrast, Kim and Kim (2001) argue that trait associations and character modularity are

highly unlikely in the space of possible combinations and hence require special explanation.

The two views can be reconciled if the reference space of the possible itself evolves in the history of individual clades. Contingency produces directionality in the form of phylogenetic constraint, and at each stage in the evolution of a particular taxon, possible morphologies are not all equally likely (Raup and Gould 1974). *Particular* character associations are highly unlikely relative to the total reference space, but it is likely that *some* associations, and perhaps many, will occur relative to a more limited set of possibilities expressed in phylogenetically circumscribed subregions of morphospace. Whether or not they do in any given instance may depend on the dimensionality of character complexes and of underlying causes, which specify the frequency of phylogenetic constraint relative to phylogenetic inertia. As Kim and Kim (2001) suggest, modularity relates to higher decomposability relative to a reference group (see also Mezey et al. 2000). Where the reference group lies in the phylogenetic hierarchy will determine the size of the reference space and the imprint of contingency on the macroevolution of modularity.

Macroevolutionary trends

Given the existence of macroevolutionary correlates of modularity, are there trends in the macroevolution of modularity? In the history of clades, is modularity more often increasing by parcellation of integrated phenotypes or decreasing by integration of parcellated phenotypes? Wagner and Altenberg (1996) suggest that in metazoans parcellation is more common, because innovation through differentiation from more generalized ancestors is frequent. This agrees with evolutionary interpretations of von Baer's laws and with the notion

that biological versatility, or morphogenetic semi-independence, seems to increase in

evolution (Vermeij 1973). At the same time, the potential for innovations seems to decrease

in metazoan history (Erwin et al. 1987; Eble 1998), as well as in the history of individual

clades (Foote 1997; Eble 1999), suggesting that integration is an important trend as well.

Whether parcellation or integration is more frequent may in fact depend on temporal scale and

hierarchical level (Jablonski 2000). The origin of bodyplans during the Cambrian radiation,

for example, can be interpreted as an increase in parcellation, since cell and tissue

specialization would have accompanied divergence from generalized colonial protozoans

(Wagner 1995) or larvae (Davidson et al. 1995). Later increase in integration of bodyplans

would follow, with formerly evolvable characters becoming developmentally entrenched as

subclades appear and diversify and new characters accumulate in hierarchical fashion (see

Eble 1998). More generally, novelty across the phylogenetic hierarchy and across scales of

time may often involve the differentiation of existing elements (reduction of serial homology,

reduction of degree of isometry) and hence some degree of parcellation. While later

persistence of novelties may be a matter of selective advantage alone, the building up of the

hierarchy of homology leads novelties to become more integrated and to be maintained by

developmental constraint. To the extent that the evolution of modularity by parcellation leads

to long-lived modules in macroevolution, later integration of such modules as homologies is

likely.

CONCLUSION

Despite its scope, morphological modularity remains remarkably understudied. Because morphology provides basic data in embryology, systematics, quantitative genetics, functional morphology, and macroevolution, and because modularity is a seemingly pervasive aspect of organization and variation, the recognition of morphological modularity as a target of empirical and theoretical study can help in generating new research questions and a more interdisciplinary discourse within biology. Morphological modules are hypotheses of individuation that may find validation in separate mechanistic or theoretical contexts, but which can also be justified on their own, in terms of the distinct evolutionary and developmental dynamics that morphology entails. Morphological modularity may be particularly important in macroevolution. Understanding it in this context will demand a shift in conceptual thinking, but the research protocols are already available. As macroevolution joins evolutionary developmental biology in the expansion of evolutionary theory, morphological modularity should become an important basis for interaction and cohesion.

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