

# Theoretical morphology: state of the art

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The morphological diversity of life has captivated systematists in the construction of classifications, embryologists in the study of development, and evolutionists in the formulation of theories of organic change. In a century marked by the advances of molecular biology, has the discipline of morphology produced anything...new? Yes. The solidification of paleontology and systematics and the emergence of macroevolution as a legitimate field owe much to an increased rigor in the analysis of morphological data. The discipline of morphology has also achieved an unprecedented sophistication through another development, the very expression of its maturity: theoretical morphology. Theoretical morphology forms the subject of McGhee's landmark book, an elegant combination of compendium and manifesto. Its richness and scope provide fodder for a critical appraisal of the discipline of morphology, particularly quantitative and developmental morphology.

### **Early Theoretical Morphology**

Goethe, the father of morphology (he invented the term), wrote in 1795 that "morphology may be viewed as a theory in and of itself" (Miller 1995, p. 57) and that "morphology may be

said to include the principles of structured form and the formation and transformation of organic bodies” (ibid.). Goethe explicitly dismissed “number and quantity” and chose to pursue qualitative statements, but his approach, which produced generalizations about the combinatorial logic of bones and plant organs, and laid out some of the early foundations of comparative anatomy, is key to theoretical morphology. Implicit in this approach, taken up by comparative anatomists such as Geoffroy Saint-Hilaire, Cuvier, and Owen, and by embryologists such as Von Baer, was the conviction that variation is bounded, that from “an infinity of distinct arrangements, diversity is limited to certain structures” (Geoffroy Saint-Hilaire 1830). More generally, an assumption of orderliness in nature and the search for natural laws guided these forerunners of theoretical morphology and their inference of unity from diversity. While this qualitative theoretical morphology preceded what we now see as an eminently quantitative discipline, its importance should not be underemphasized: the principles and the conceptual framework laid out by comparative anatomists and embryologists in the last two hundred years are as fundamental to the development of theoretical morphology as mathematical sophistication in itself.

The rise of Darwinism and Mendelism produced theories of a different kind, relevant to the understanding of morphological variation but devoid of the spirit of theoretical morphology. Morphology ceased to elaborate the theoretical stance (Bateson 1896 and Thompson 1917 being the lonely exceptions); rather, it was population genetics that emerged as a distinctly theoretical

discipline through the works of Fisher, Wright, and Haldane. It was not until after the Modern Synthesis that quantitative theoretical morphology saw its full expression in the works of Raup (e.g., Raup 1966; Raup and Michelson 1965).

### **Modern Theoretical Morphology**

McGhee provides a potentially unifying characterization of theoretical morphology as comprising (1) the mathematical simulation of form and (2) the construction of morphospaces where the possible and the actual can be represented and compared. The simulation of form may or may not be accompanied by morphospace construction, but, as McGhee indicates, morphospace comparisons of theoretical and empirical distributions are the major contribution of theoretical morphology to the study of evolution. Accordingly, more than half of the book is dedicated to a detailed description of theoretical morphospaces of branching, accretionary, and discrete growth forms, with extensive discussion of both model parameterization and empirical filling of theoretical morphospace. In addition, the simulation of form may not always take morphogenesis explicitly into account, but modeling of growth and development is sometimes the primary goal of theoretical morphological studies. Explicit morphogenetic models are treated separately, if somewhat more briefly, after the discussion of theoretical morphospaces. All in all, a splendid review is provided, one which is critical, well-articulated, historically exhaustive, and stimulating in its suggestions for future research. The literature of theoretical

morphology is quite large (see Reif and Weishampel 1991) – McGhee’s is now the best introduction to the core of this literature and to the field as a whole.

For the more conceptually oriented reader, for those who have thought at length about morphospaces, their meaning, and their utility, and for researchers looking for immediate insight into the field of theoretical morphology as well as inspiration for future research, chapters one (“What is theoretical morphology?”), two (“The concept of theoretical morphospace”), seven (“The time dimension: evolution and theoretical morphospaces”) and eleven (“The future of theoretical morphology”) are indispensable and may well be read separately in their own right. The status and larger implications of theoretical morphology as conceived by McGhee are clearly laid out there, and rely extensively on distinctions carved in the disciplinary landscapes of morphology and macroevolution. Whether the distinctions made are the only ones possible, and whether the nature and scope of theoretical morphology is unambiguous, remains open to debate.

### **Theoretical Morphospaces and Empirical Morphospaces**

The distinction between theoretical and empirical descriptions has a potentially central position in morphospace studies. Theoretical morphospaces are able to represent what is possible, or occupiable, and empirical morphospaces are renditions of what has actually been occupied (McGhee 1991; Arthur 1997). The distinction is further magnified when presented in the manner chosen (and emphasized) by McGhee: theoretical morphospaces are based on

mathematical parameters, “pure and pristine” in the absence of any measurement data; empirical morphospaces are based on statistical constructs highly dependent on sample size, character choice, and the production of multivariate ordination spaces. Thus, theoretical morphospaces can be characterized by the “ability to specify nonexistent form” (p. 13), and by the dimensions being “geometric or mathematical abstractions of form” (p. 14) which are based on a mathematical model.

In terms of the “time dimension”, McGhee argues that “the techniques of theoretical morphospace analysis are particularly well suited to analyzing the evolution of morphology in time” (p. 183), and for “the study of the relationship between taxonomic and morphologic diversity (...), as the dimensions of a theoretical morphospace are sample independent, which is not the case for empirical morphospaces” (p. 190). Implicit is the suggestion that extinction, trends, and disparity changes in morphospace cannot be reliably studied in empirical morphospaces.

These distinctions are useful because they suggest a domain of application for theoretical morphology which is distinct from many empirical studies. However, they rely on the explicit definition of empirical morphospaces in terms of multivariate ordination. McGhee is thoroughly consistent in his discussion of empirical morphospace analyses in these terms. Yet what could be termed “empirical morphology” (morphometrics, disparity studies, constructional morphology, functional morphology) is quite often practiced in strictly vernacular fashion, with

study objects (actual organisms) taking precedence over method of study, and ordination becoming an optional tool. And even when ordination is used, some of its potential limitations may be avoidable. There are thus nuances to empirical analyses in macroevolution which, while perhaps not directly relevant in the context of the simulation of morphology as a touchstone of theoretical morphology, are important in an expanded characterization of the scope of different morphospace studies and their interrelationship.

(1) Ordination. Sample-dependence and the issue of cross-sample comparability complicate macroevolutionary inference in ordination analyses, particularly when different ordination studies are contrasted. The challenges are not unsurmountable, however, if statistics that explicitly take into account sample size, scale of measurement, and dimensionality are used (see Sneath and Sokal 1973; Van Valen 1974), and if the comparisons themselves are performed in a statistical framework. Incommensurable ordinations can thus still be compared in terms of levels of clustering, discreteness, and dispersion. In individual studies, the problem of comparability can be eliminated with analysis of the total sample, with a posteriori sorting of species through time (e.g., Foote 1993, 1999; Wills et al. 1994; Roy 1994; Dommergues et al. 1996; Saunders and Work 1996; Wagner 1996; Eble 2000). In this way, the reference state space does not change (at least in the context of the study), and meaningful analyses can always be performed if relative statements are emphasized. Sample-dependence is a more difficult problem, and as McGhee indicates, it leads to an inherent instability of ordination axes. Of

interest then is the degree of instability relative to sample size. This issue could be explored with artificial datasets, and it may well be that particular modes of evolution (see Fisher 1986; McShea 1994; Foote 1996) would render measures of location and dispersion asymptotically stable even if an arbitrary number of nonexistent morphologies were to be taken into account. Ideally, one expects that the statistical inference of macroevolutionary pattern and process from ordination studies converges, however inexactly, on the more exact (if model-dependent) conclusions that can be drawn from analyses of theoretical morphospace occupation. Simultaneous studies of theoretical and ordination morphospaces addressing issues pertaining to both could help clarify the scope of each approach.

(2) Raw morphospaces. When multidimensional morphospaces of actual organisms are studied, ordination techniques are used to reduce dimensionality and facilitate graphical representation. But the original reference space is not contingent on ordination. Raw morphospaces, conceived in terms of observed morphological variation but before any data-driven multivariate analysis, can often be used to derive state space portraits (e.g., variance and range) of actual morphologies in a manner that is not subject to the sample-dependent statistical projections characteristic of multivariate ordination (e.g., Foote 1993, 1995, 1999). They complicate the theoretical/empirical dichotomy in interesting ways. Raw morphospaces are empirical in the sense that their dimensionality is based on induction from observation, i.e., continuous or discrete variables are enumerated so as to capture various aspects of real form.

But raw morphospaces are also theoretical because they can represent nonexistent form, even in the absence of a model (see Thomas and Reif 1993; Foote 1995). They are not theoretical in the restricted sense of relying on a generative mathematical model, and therefore do not fit one of McGhee's criteria, but they always have the potential to represent a spectrum of possibilities that is either logically finite (discrete character morphospaces, continuous character morphospaces which are size-standardized) or biomechanically finite (even without standardization, the range of continuous variables falls along definite, however approximate, limits, as extremes in size can often be predicted on bioenergetic grounds in clades where knowledge about the allometry of physiological parameters exists). For example, if a coding scheme is cast in terms of 3 binary variables  $x, y, z$ , then a finite morphospace is immediately implied (the locations being 000, 100, 110, 111, 011, 001, 010, and 101). The "morphologies" are theoretical possibilities (implied by the finiteness of the raw morphospace, not by simulation) which can be compared with the range of actual form. As dimensionality increases, one may choose to use ordination to economically represent and interpret the data, but the original, raw character state space is invariably theoretical in its incorporation of nonexistent possibilities. And if the raw morphospace is constructed with the aid of a morphogenetically motivated conceptual model (e.g., Thomas and Reif 1993), the full spirit of modern theoretical morphology as conceived by McGhee is recaptured. Thus, although the mathematical simulation of morphology can simplify our

representation (and explanation) of variation, the study of the evolution of the actual in the realm of the possible can derive important insights from raw morphospaces.

(3) Disparity. Disparity is an inherently empirical property, for it concerns the actual variability of samples across intervals, whether the reference scale is empirical or theoretical. Different scalings might, for example, affect how extremes in morphology are interpreted (e.g., Foote 1995 on poteriocrine cladid crinoids), but careful data analysis (e.g., with resampling techniques) often allows robust qualification of the results, even when ordination is used. In fact, different scalings may well converge if saturation of morphological space can be documented (Foote 1995, 1996, 1997). When disparity is quantified in terms of the original variables, it will directly measure morphospace occupation relative to a theoretical gamut of possibilities, derived from either a mathematical (geometric) or a conceptual (enumerative) scheme. The main difference will usually be dimensionality, with minimization being desirable in a mathematical model and maximization desirable in an enumerative representation. Both can be useful in studying the evolution of disparity, and in resolving debates such as the one on Cambrian disparity (Gould 1989, 1991; Briggs et al. 1992; Foote and Gould 1992; McShea 1993; Conway Morris 1998), as the issue of what happened (increase, decrease, or maintenance of disparity) is distinct from the issue of how it happened or what could have happened (the degree of contingency of disparity dynamics). Theoretical morphology holds great promise for a better understanding of the latter. Theoretical morphospaces, by specifying bounds within which

contingency must operate, can represent the possible maximum range and variance of aspects of form, and when this information is available unique mechanistic inferences about constraints and their differential temporal expression can be made. Empirical morphology, in turn, remains necessary for the proper quantification of temporal patterns of disparity. To the extent that high dimensionality is real, the disparity of form is best quantified in many dimensions.

### **Theoretical Morphology and Developmental Morphology**

It is seldom appreciated in theoretical morphological research that most models that have been produced to simulate form and morphospace imply only heterochrony, but not heterotopy, thresholds, or more generally, major innovation. Theoretical morphology models often imply only heterochrony because while the magnitude of parameters is varied in the simulations, the parameters themselves never change within a given group. They are thus limited by the extent to which innovation is taken into account, and by how innovation itself is defined. If innovation is defined as a jump in theoretical morphospace, it may be possible to describe its dynamics with standard models even if the implied heterochronic shifts turn out to be correlates of other developmental events. If, however, innovation is defined as a nonheterochronic event (Rice 1997), more elaborate geometric models become necessary. Major nonheterochronic innovation is not readily accommodated because the implied shifts in complexity often defy the desideratum of mathematical simplicity.

Innovation is extremely important in understanding macroevolution, however (Jablonski and Bottjer 1990; Müller and Wagner 1991; Erwin 1994). Although the proper representation of innovation also poses a challenge to empirical morphospace studies, it has become increasingly apparent that, often, empirical morphospaces are the only tractable way of producing a sufficiently comprehensive understanding of form change in groups where complexity is high, in other words, where the number of characters is high (see Foote 1992; 1999). When innovation is frequent, dimensionality itself evolves, complicating the task of devising models that are simple and realistic at the same time. In such cases, the empirical study of variation in ontogenetic trajectories and of how growth is regulated can be very useful in suggesting appropriate models. To this end, what is needed is a comprehensive formalization of the ideas of innovation and heterotopy (Rice 1997; Zelditch and Fink 1996; Raff 1996; Hall 1998) into analytical toolboxes analogous to those of heterochrony (Alberch et al. 1979; McKinney and McNamara 1991; Godfrey and Sutherland 1995).

On the one hand, theoretical morphological studies of more complex morphologies may be most successful with an initial focus on particular subclades, for which more detailed developmental data can be harnessed. On the other hand, it may be that the future of theoretical developmental morphology will reside in the sophistication of the underlying mathematics itself, with (1) complementation of classical linear models with nonlinear ones, and (2) the use of models which can themselves evolve, by incorporating nonuniform components of

morphological change (see Rice 1997). For example, if certain organisms grow fractally (Lindenmayer 1968; Prusinkiewicz and Lindenmayer 1990; Kaandorp 1994), then fractal growth models become more realistic. If innovation is present, the exploration of nonlinear dynamical models with explicit thresholds and bifurcation points, and sensitivity to small parameter changes (e.g., Oster and Alberch 1982; Nijhout 1994), might be instrumental in the analysis of morphologies with many interacting components and complicated genotype-phenotype maps. Finally, the use of genetic algorithms (Mitchell and Taylor 1999) and likelihood approaches (Edwards 1992) to maximize the fit of models to data might allow models of morphology to evolve along with the simulation of organisms, i.e., for the mathematical structure of theoretical morphological models to change as nonheterochronic innovations (nonuniform components of change) accumulate through evolution.

Future advances in theoretical morphology may thus hinge on closer collaboration between theoreticians and developmental morphologists, to ensure realistic model parameterization. McGhee discusses some of these issues in connection with physicochemical developmental models, where different views on morphogenesis (reaction-diffusion, mechanochemical, etc.) may lead to alternative models that fit the data equally well, and are difficult to distinguish in the absence of experimental evidence. In the long run such issues are relevant to all theoretical morphology models and the nature of their falsifiability in general (see Raup 1969).

### **Theoretical Morphology and Adaptation**

There is no necessary link between theoretical morphology and adaptation. This point is made abundantly clear by McGhee, who emphasizes that differential occupation of theoretical morphospace is silent about adaptation. Theoretical morphology is about form and possibility; adaptation is about function and efficiency in the realm of the actual. Adaptation can certainly shape the occupation of morphospace; but because the model underlying a morphospace can produce nonfunctional possibilities, the morphogenetic process itself is nonadaptive. For example, some accretionary shells are dysfunctional; others are functional; but accretion is afunctional, it is a developmental constraint. Accretionary growth may have originally appeared gradually as an adaptation, or it may have appeared as a sudden developmental innovation; after appearing, it was maintained in prospective independence from adaptation. Thus, when stasis of parameters in a model is assumed at the outset (the model does not evolve), the parameters themselves cannot be adaptive, only their values can.

Is functional analysis a necessary step in theoretical morphology? McGhee indicates that analysis of functional significance is an optional tool in interpreting morphospace distributions, but suggests that it should be the next step after morphospace construction and mapping. To be sure, this is the default approach in evolutionary research. Yet differential filling and density of actual occupation of different regions in morphospace may also reflect historical contingency,

historical constraint, and developmental constraints based on either model parameters or unconsidered generative parameters (Raup 1972, 1987; Maynard Smith et al. 1985; Kauffman 1993). These issues suggest the desirability of complementing functional analysis of morphospace filling with approaches such as stochastic simulation of morphological evolution (e.g., Raup and Gould 1974; Foote 1996), mapping of phylogenies onto morphospaces (e.g., Bookstein et al. 1985; David and Laurin 1996; Wagner 1997; Eble 2000), explicit assessment of morphogenetic significance of distributions (e.g., how the distributions relate to heterochronic and nonheterochronic change), and modeling based on more refined developmental parameters, where renditions of form are not all equally likely (Goodwin and Trainor 1983; Shubin and Alberch 1986; Alberch 1989; Webster and Goodwin 1996; Rice 1998). A plurality of approaches is heuristically justified, such that the steps of functional analysis, developmental analysis, historical analysis, and stochastic modeling deserve more proportionate attention in the analysis of morphospace occupation (whether this in fact happens is contingent on the interests of the investigator). A commitment to pluralism thus approximates theoretical morphology to constructional morphology or morphodynamics (Seilacher 1970; 1991).

Are morphospaces ever adaptive landscapes? Careful functional analysis may validate clusters in morphospace as targets of selection, but this can hardly transform a morphospace into an adaptive landscape. First, since in most theoretical and empirical morphospace studies species distributions are depicted, any interpretation of distributions that relies solely on one

mechanism (organismic selection) overlooks the potential impact that differential speciation and extinction rates, and their various controls at the focal level and at different levels in the hierarchy, may have on observed distributions. Morphospace distributions are products of macroevolution, and as such will likely respond to the plethora of multilevel evolutionary processes even when functional explanations can be advanced. Second, species may often not be meaningful entities in an adaptive landscape, because if only demes have niches, only demes can have adaptive landscapes (Eldredge 1989), which is actually what Sewall Wright originally intended to represent (Provine 1986). Whether morphospaces can ever be seen as adaptive landscapes may ultimately depend on the fate of debates concerning the nature of competition in macroevolution (Benton 1987; Sepkoski 1996; Gould 2000).

### **Theoretical Morphology and Macroevolutionary Theory**

Can we uniquely characterize protocols for theoretical research in morphology, and more generally, macroevolution? Research protocols and conceptual schemes are useful in the delimitation of fields of enquiry such as theoretical morphology. But the ingredients of theoretical morphology are also found in other morphological disciplines, as the objects of explanation (e.g., actually or potentially evolving organisms) and the strategies of explanation (e.g., model building) often circulate across disciplinary boundaries. This suggests that the many research opportunities in theoretical morphology can be fruitfully complemented with other

kinds of macroevolutionary research. Further understanding of morphospace mechanics, for example, may hinge on a more interdisciplinary morphology and on the articulation of multiple morphospace approaches, such as combination and hybrid studies (Chapman et al. 1996) and studies that transcend the theoretical/empirical distinction by emphasizing function (e.g., Hickman 1993) or development (e.g., Eble 1998).

Conversely, empirical morphology has theories for disparity profiles, morphospace occupation, phylogenetic structure, etc., which can inform the analysis of empirical data in theoretical morphospace studies. In addition, as argued earlier, raw morphospaces can often make implicit a theoretical morphospace, because unrealized possibilities can be considered. The portrayal of possibilities is an inherently theoretical activity, one which most morphologists, ever since Goethe, have tackled to different degrees. Perhaps an absolute separation between theoretical and empirical morphology is possible under a particular definition of theoretical (the use of mathematical models of form), but to the extent that the study of morphospace possibilities and actualities is emphasized, productive overlap accrues. The latter is arguably more important in macroevolutionary theory, because it allows incorporation of a broader range of model types (physical, conceptual, statistical; see also Raup 1972; Hickman 1993). Whether a theoretical morphospace should be defined by its content (depicted or implied theoretical possibilities) or by the method of its construction is an open issue, which may well be resolved on a case-by-case basis, at the discretion of the investigator.

Macroevolutionary theory is a composite of diverse theoretical approaches, with theoretical morphology standing as its most elegant, if still understudied, expression. In empirical morphology, theories are often historical and statistical, because time is an important component of explanation and chance an element of evolution. Theories in theoretical morphology, conversely, are often focused on mathematical modeling and tend to be ahistorical, deterministic, and mechanistic. Theoretical morphology is best understood in the context of disciplines where stability is a major topic of theoretical work – physics, chemistry. A primary concern with order and rational transformation underlies such disciplines, much as in structuralism as a way of seeing (Lambert and Hughes 1988). In structuralist research, there is a fundamental commitment to the study of the possible, with locations in state space prevailing over their actual occupants (Deleuze 1973). “State space thinking”, whether structuralist or not, is also found elsewhere in biology (e.g., Maynard Smith 1970; Goodwin 1990; Kauffman 1993; Wagner and Altenberg 1996; Webster and Goodwin, 1996; Fontana and Schuster 1998; Maurer 1999). Therefore, feedback between theoretical morphology and other state space approaches in biology holds much promise.

Work on theoretical morphology is still limited relative to empirical morphology. McGhee’s contribution goes a long way towards rectifying this state of affairs and inspiring a new generation of theoretical morphologists. The growth of theoretical morphology and its effective articulation with other morphological subdisciplines is needed for the full reemergence

of morphology as the synthetic discipline of form at the core of macroevolution. As our knowledge of macroevolution increases, it is important to take into account form and its modeling in full.

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