What Is Theoretical Morphology?

Depending on your point of view, theoretical morphology is either a very new field of study or a very ancient one. The term "theoretical" morphology was first used by E. S. Russell in his classic book *Form and Function: A Contribution to the History of Animal Morphology* more than eight decades ago (Russell [1916] 1982:33). In addition, Lauder (1982:xviii) argued:

*Form and Function* demonstrates the antiquity of many issues being debated today. For example, the notion that extant organismal forms are only a subset of the range of theoretically possible morphologies (referred to as theoretical morphology; see Raup and Michelson 1965, McGhee 1980[b]) can be found in the writings of Cuvier.

It is also true that theoretical geometric models of natural morphology are not new, and neither is the debate over whether model or parameter is biologically more appropriate (e.g., the debate between Moseley [1838, 1842] and Naumann [1840a,b; 1845]).

What is understood as theoretical morphology today, however, was generally not feasible until the advent of the computer. Two quite dif-

What is Theoretical Morphology?

Different conceptual areas of evolutionary biology are understood today under the umbrella term of theoretical morphology: (1) the mathematical simulation of organic morphogenesis and (2) the analysis of the possible spectrum of organic form via hypothetical morphospace construction. The second concept follows from the first but has quite different goals.

In the first conceptual area, the initial focus in the early days was to model existent form with a minimum number of parameters and mathematical complexity. In essence, the goal was to reveal general and common geometric principles in what, at first glance, might appear to be widely divergent organic morphologies (such as those exhibited by ammonites and brachiopods). More recent work in this area of theoretical morphology models the actual process of biological morphogenesis itself.

In the second conceptual area, the goal is to explore the possible range of morphologic variability that nature could produce by constructing \( n \)-dimensional geometric hyperspaces (termed "theoretical morphospaces"), which can be produced by systematically varying the parameter values of a geometric model of form. Such a morphospace is produced without any measurement reference to real or existent organic form. Once constructed, the range of existent variability in form may be examined in this hypothetical morphospace, both to quantify the range of existent form and to reveal nonexistent organic form. That is, to reveal morphologies that theoretically could exist (and can be produced by computer) but that never have been produced in the process of organic evolution on the planet Earth. The ultimate goal of this area of research is to understand why existent form actually exists and why nonexistent form does not.

The founder of modern theoretical morphology was David M. Raup, who first used the term in 1965 in a paper written with A. Michelson. Although Raup was using theoretical morphology in the first conceptual sense in his earlier papers (Raup 1961, 1962), the term theoretical morphology itself was originally used in only the second conceptual sense, as can be seen in the brief (two-sentence) abstract of their classic Science paper "Theoretical Morphology of the Coiled Shell": "In studying the functional significance of the coiled shell, it is important to be able to analyze the types that do not occur in nature as well as those represented by actual species. Both digital and analog computers are useful in constructing accurate pictures of the types that do not occur" (Raup and Michelson 1965:1294). Later, however, Raup explicitly expanded the usage of the term theoretical morphology to cover modeling or simulation of the actual process of biological morphogen-
sis itself, as seen in his paper "Theoretical Morphology of Echinoid Growth": "The computer model also has little biological basis, but, because it succeeds in simulating morphology (and ontogenetic development), we may conclude that the actual biological system controlling plate patterns need not be more complicated than that used in the computer simulation" (Raup 1968:62; italics Raup's).

THE DISCIPLINE OF THEORETICAL MORPHOLOGY AND ITS GOALS

Morphospace is potentially one of paleontology's most significant contributions to the analysis of form. It is the tool by which we can document the range of actual structures that have evolved in the history of life as a subset of the structures that are theoretically possible.

Hickman (1993b:170)

Of the two research goals of theoretical morphology—the creation of theoretical models of morphogenesis and theoretical morphospace analyses of the evolution of organic form—it is the latter that has received more attention and that has been hailed as the greater contribution to our understanding of how evolution works. I have therefore decided to consider theoretical morphospaces first. In chapter 2 we shall examine in detail the fundamental concept of the theoretical morphospace and how a theoretical morphospace is constructed. Then, in chapters 3 through 7, we shall examine actual case studies of theoretical morphospace analyses. Only in chapter 8 will we consider the goal of theoretical models of morphogenesis, first with an example in that chapter of how mathematical models are constructed and then with the examination of the many different theoretical morphogenetic models in chapters 9 and 10.

We shall now approach the question, What is theoretical morphology? from a different perspective by considering what it is not. Theoretical morphology is not morphometrics or functional morphology or constructional morphology.

THEORETICAL MORPHOLOGY AND MORPHOMETRICS

Theoretical morphology differs from biometrics or biostatistics as it searches for the essential geometric growth rules in any particular case.

De Renzi (1995:241)

Morphometrics is a school of morphologic analysis concerned with the precise measurement of form in individual organisms and with
the precise comparison of those measurements among different individuals. It is the school of morphometrics that is most frequently confused with theoretical morphology. This confusion is likely due to the fact that both morphometrics and theoretical morphology are highly mathematical and that both schools extensively use computers. However, the goals and techniques of theoretical morphologic analyses and morphometric analyses are profoundly and fundamentally different.

Because morphometrics is concerned with the precise quantification of existent morphology, it often seeks to reproduce form as a sort of mathematical picture by means of various mathematical techniques of shape analysis and outline-fitting algorithms. But morphometrics does not simply seek to precisely portray existent morphology via quantification; it is even more concerned with the precise quantitative comparison of multiple existent morphologies which may vary in form to a greater or lesser degree. Thus morphometric analyses are often characterized by the intensive examination of existent morphology to discern homologous features from analogous ones and to separate synapomorphic characters from symplesiomorphic ones. And that is extremely important if we are to obtain an accurate picture of the morphologic changes that have taken place in the evolution of a group of organisms and if we are to construct phylogenies for those organisms that are holophyletic, phylogenies that accurately reflect ancestor-descendant relationships.

An early inspiration for morphometrics was D'Arcy Thompson's coordinate transformation method of shape comparisons (1917, 1942). Over the many years since his work, morphometricians have devised even more precise methods of shape quantification and comparison, from simple bivariate plots to multivariate hyperspaces, from Fourier series to fractals (Mandelbrot 1983; see Lutz and Boyajian 1995). The morphometric literature is enormous and cannot be summarized here. Suffice it to say simply that morphometrics is fundamentally concerned with quantification.

In contrast, theoretical morphology is interested in simulation, not in quantification. Theoretical morphology is concerned with the simulation of the principal aspects of form with a minimum number of geometric parameters, or with the simulation of the morphogenetic process itself that produced the form under study, and is not concerned with the production of a precise mathematical characterization or picture of any given existent form. In fact, the creation and examination of nonexistent form is often of more interest in theoretical morphologic analyses than the examination of existent form.

The second major goal of theoretical morphology is the construc-
tion of \( n \)-dimensional geometric hyperspaces called theoretical morphospaces. The mathematical techniques of morphometrics have also been used to make hyperdimensional morphospaces, typically by applying ordination techniques to matrices of measurements taken from existent organisms. These hyperspaces I have termed "empirical morphospaces" (McGhee 1991), as opposed to "theoretical morphospaces," as they are fundamentally different from theoretical morphospaces. To mention just one such difference, an empirical morphospace does not exist in the absence of measurement data, whereas a theoretical morphospace does. The differences between these two types of morphospace will be explored in greater detail in chapter 2.

THEORETICAL MORPHOLOGY AND FUNCTIONAL MORPHOLOGY

Although theoretical morphology does not play a direct role in the inference of function in fossils, it can be used to generate and organize functional hypotheses and to compare the range of designs that have evolved with what is theoretically possible. 

\[ \text{Hickman (1988:790)} \]

Functional morphology is a school of morphologic analysis that specifies the functional or adaptive aspects of organic form, usually by employing the paradigm methodology of Martin J. S. Rudwick (1964; see also the review in Lugar 1990). The paradigm methodology is a formalized technique of mechanical analogy in investigating the functional significance of an organic structure or form. Several functions are first postulated for the structure under investigation, and then the optimal mechanical design for each function is determined (the paradigm). The paradigm form that most closely matches the original structure is considered to demonstrate the actual function of the structure.

It cannot be denied that much of organic form has adaptive significance and represents an adaptation. That fact does not mean that all organic form is adaptive, however, as we shall see in the next section, on constructional morphology. Using the paradigm methodology to analyze the adaptive significance of organic form has been sharply criticized by some (Gould and Lewontin 1979), and the very logic of the methodology itself has been declared invalid by some (Signor 1982) and carefully validated and justified by others (Fisher 1985).

Functional morphology is used in the latter stages of a theoretical morphospace analysis when the adaptive significance, if any, of the distribution of real organic form in a theoretical morphospace of hypothetical form is examined (to be discussed in chapter 2). But functional
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Morphology is generally not used at all in the theoretical modeling of morphogenesis. That is, functional morphology is a separate and valuable tool that may or may not be used in theoretical morphologic analyses.

THEORETICAL MORPHOLOGY AND CONSTRUCTIONAL MORPHOLOGY


Seilacher 1970:395

Constructional morphology is a school of morphologic analysis founded by Adolf Seilacher (1970; see also the review in Thomas 1979). In constructional morphologic analyses, organic form is postulated to result from the interplay of three constraints or limiting factors: functional (adaptational) constraints, fabricational (morphogenetic) constraints, and historical (phylogenetic) constraints. At the time (in the late 1960s) the school of constructional morphology was founded, this threefold concept of form was a view of morphology radically different from that held by most American and British morphologists, who tended to see all morphology as the result of adaptation (a point of view that came to be termed "hyperselectionist" by Raup [1972] and "adaptationist" by Gould and Lewontin [1979]; see also the review in Gould [1995]). And indeed, the fundamental assumption of the school of functional morphology is that morphology does have a function.

In contrast, Seilacher (1970, 1973) suggested that many aspects of morphology might be side effects of the process of morphogenesis itself, the "fabricational noise" of growth constraints, and not the result of adaptation. In addition, Seilacher (1970) proposed that other aspects of morphology might be the result of phylogenetic constraint, the result of genetic legacy, and also thus not the result of adaptation. Both morphogenetic constraints and phylogenetic constraints are rooted in the concept that organisms possess an evolutionary Bauplan. Bauplan is an engineering German term that has been variously translated as "ground plan," "blueprint," or "engineering design." In biology, the term is used to represent the basic architectural and organizational
pattern shared by the members of a monophyletic clade of higher taxonomic rank. To quote Valentine (1986:209): “At the upper levels of the taxonomic hierarchy, phyla- or class-level clades are characterized by their possession of particular assemblages of homologous architectural and structural features; in this paper, it is to such assemblages that the term Bauplan is applied.”

The definition of the term Bauplan is not tied to any specific taxonomic rank, and so its usage varies from clade to clade and to subsets of clades within clades. Valentine (1986), for example, uses the term Bauplan to refer to the assemblage of architectural features shared by organisms at the phylum or class level, and within these Baupläne he uses the term Unterbauplänne to refer to distinctive major subtaxa at the class or ordinal level, the next taxonomic level down from the initial designation of the Bauplan.

It is generally agreed that Bauplan refers to an assemblage, or complex, of architectural features and not to just one distinctive morphologic feature characteristic of a particular higher taxon. Because I am well aware of that general agreement, I must, at this point, take exception to Hall, who wrote: [1996:226]

For others, the term Bauplan is applied to a single morphological structure within a group, as in the morphology and growth of brachiopod valves (McGhee 1980b) or the circuitry of the nervous system (Ebbesson 1984). However, this is not consistent with the essence of the concept of a suite of characters that unites members at higher taxonomic levels. Woodger (1945) discussed this issue and clearly came down against Bauplänne applying to individual elements.

In reference to this study of the morphology and growth of brachiopod valves (which is covered in chapter 5), I specifically stated: “The planispiral shell of the Brachiopoda can be viewed as an integral part of the Bauplan of the phylum, its basic engineering design” [McGhee 1980b:62]. That is, the shell is an integral part of the Bauplan of the phylum Brachiopoda, not the Bauplan itself. The concept of the Bauplan of the phylum Brachiopoda as an assemblage of features is made even more explicit in McGhee (1980b:62–63):

Some aspects of the articulate brachiopod Bauplan which will be of importance in subsequent discussions are: (1) shell growth by terminal accretion without major modification after deposition of shell material, (2) the presence of two valves in articulat-
WHAT IS THEORETICAL MORPHOLOGY?

In a constructional morphologic analysis, Seilacher (1970) clearly identified the school of theoretical morphology with the analysis of the morphogenetic, or fabricational, constraints on organic form (Bautechnischer Aspekt). And as can be seen in the quotation from his classic paper at the beginning of this section of the chapter, he clearly indicated that both aspects of theoretical morphology (morphogenetic simulation and morphospace construction) were to be so considered. Likewise, Seilacher (1970) clearly identified the school of functional morphology with the analysis of the functional, or adaptational, constraints on organic form in a constructional morphologic analysis. The school of constructional morphology was thus envisioned as a synthetic one, incorporating the disciplines of functional and theoretical morphology and the German concept of evolutionary Bauplan.

Since Seilacher's (1970) early visualization of form as a result of the interplay of these three factors, other morphologists have added additional factors (Raup 1972, Hickman 1980). Seilacher (1991) himself expanded the concept of constructional morphology to a concept of "biomorphodynamics" by adding an environmental factor to his previous three morphologic ones.

As a graduate student in 1977, after my first stay of research at the University of Tübingen with the Konstruktionsmorphologie research group and many conversations with Seilacher, I wrote in my dissertation: "The synthetic school of constructional morphologic analysis encompasses the paradigm methodology of Rudwick (1964, 1968) and the theoretical morphologic approach of Raup and Michelson (1965)." Dave Raup, my doctoral mentor, read this assessment and made no objection. After more than two decades of thought and research, however, I now view constructional morphology as more a heuristic concept, a working hypothesis, than a specific analytic methodology. In my experience, most morphologists concentrate on the three separate aspects of constructional morphology separately rather than synthesizing them together. That is, functional morphology has remained
WHAT IS THEORETICAL MORPHOLOGY?

Functional morphology, and theoretical morphology has remained theoretical morphology.

THE CURRENT STATE OF THE SCIENCE OF MORPHOLOGY

The ultimate triumph of theoretical morphology would be an understanding of biological diversity, framed in terms of the boundaries between the possible and the actual and the possible and the impossible. It should integrate across all levels of structure, from organic molecules to entire and seemingly complex functioning organisms, where as yet undiscovered laws of structural consonance may exist.

Hickman (1993b:170)

The ultimate triumph of theoretical morphology is not even in sight! Consider this optimistic prediction, made almost three decades ago: "A science of form is now being forged within evolutionary theory. It studies adaptation by quantitative methods . . . it seeks to reduce complex form to fewer generating factors and causal influences" (Gould 1970:77). Gould was not referring to morphometrics when he mentioned "quantitative methods" but, rather, the techniques of theoretical morphology and their power in the study of adaptation (or non-adaptation, for that matter). And even though considerable progress has been made in theoretical morphology in the past three decades, it is a fact that more quantitative morphologists today pursue morphometrics than theoretical morphology.

Morphometrics is a very valuable and important school of morphologic analysis, with its own specific goals and techniques. In contrast with popular field of morphometrics, the analytic techniques of theoretical morphology have been sadly neglected. One of the goals of this book is to make clear to the reader the conceptual difference between the goals and techniques of morphometrics and those of theoretical morphology and to reveal to the reader those aspects of the evolution of life on Earth that are ideally suited to theoretical morphologic analyses, but not to morphometric analyses.

In the last chapter of this book, I shall outline a challenge, particularly to graduate students, for the development of theoretical morphology in the future. There are so many interesting things to be done in the field, and we have barely begun to understand the evolution of form on Earth. Many excellent Ph.D. dissertations and intellectually stimulating life careers simply await the attention of bright young graduate students.