Introduction

This book is about a desire: the strong desire to develop a science of form (or "morphology"), which, with varying intensity, pervaded twentieth-century biology and reverberated into the twenty-first century. Diverse biologists sought to (re)-establish the study of form as an independent, legitimate, and key biological discipline.[1] However, their overpowering desire for morphology was punctuated by a series of failures. Most of the attempts undertaken indeed failed dramatically. This book narrates how morphologists sought to overcome a series of failures to call attention to the notion of organic form and the dynamics of its structural changes over time, and how they strove to develop the science of form as a transdisciplinary methodology on the edge of evolutionary biology, engineering, and philosophy.

Despite a succession of shortcomings, a particular structuralist, or what I call an architectural approach to form, was eventually able to sneak into mainstream evolutionary biology starting at the end of the 1960s. German- and Italian-speaking biologists[2] were at the forefront of uncovering form structures not easily reducible to natural selection alone. This rich morphological tradition would contribute to the shift in focus in evolutionary biology "from constraints on morphology to the mechanisms that enable or explain morphological evolution—so-called evolvability."[3] This culminated in the integration of morphology into

evolutionary developmental biology[4] and constituted one of the several pillars of the recent "extended evolutionary synthesis."[5]

This book traces this neglected genealogy of the science of form in depth, presenting this theory's history for the first time. More specifically, it examines how morphological investigations were either sidelined or integrated into broader biological frameworks and research programs of the twentieth century and how morphologists worked on their conceptual framework and practices to participate in the writing of the agenda of twentieth- and twenty-first-century evolutionary theory. As a result, twentieth-century morphology and specifically the architectural or structural approach to organic form played a key role in the expansion of evolutionary biology and, more broadly, in the dynamic of biologically inspired knowledge production, thus supporting the development of disciplines situated between architectural design and biology.

The importance of morphology for biology goes back to eighteenth-century polymath Johann Wolfgang von Goethe (1749–1832). He coined the term *morphology* in 1796 and defined it as the study of "form, formation, and transformation of organisms."[6] Goethe conceived morphology as a transdisciplinary science, which could be applied to many disciplines, ranging from natural history to literature and architecture.[7] Furthermore, he identified the essential aspects and methods of morphology. As he prominently put it, "If we want to introduce a morphology, we must not speak of form, but, if we need the word, we must at most think only of the idea, the concept, or of something that is fixed in experience only for the moment. What is formed is immediately transformed again, and, if we want to arrive at some degree at a living contemplation of nature, we must keep ourselves so mobile and pictorial, after the example with which it proceeds to us."[8] Following Goethe's insights, at the beginning of the nineteenth century, morphology was applied to areas other than natural history such as crystallography, geology, linguistics, and even mechanical engineering.[9]

The second important episode in the history of morphology is the advent of the methodologies proposed by Ernst Haeckel (1834–1919) and Carl Gegenbaur (1826–1903). Historians have described at length the importance of the Haeckel-Gegenbaur school for twentieth-century morphology. According to Haeckel, morphologists' task was to draw accurate phylogenetic trees that represent emerging forms through their development over time. In the second edition of his *Grundzüge der vergleichenden Anatomie* (Principles of comparative anatomy, 1879), Gegenbaur underwrote the same mission. He admitted that morphologists sought to reconstruct the natural system of the living forms to portray phylogenetic relationships. In both Haeckel's and Gegenbaur's views, Charles Darwin's theory of evolution contributed a needed framework to morphology to

accomplish this new and important task. At the same time, the drawing of phylogenetic trees could be used to corroborate Darwin's theory. As Gegenbaur put it, "The theory of descent underpins comparative morphology with the universal principle of causality, while the success of comparative morphology provides one of the most important pillars in support of the theory of descent."[10]

Simultaneously, starting from the mid-nineteenth century, morphology as an aspect of different research areas was marginalized. The science of form was accused of being too descriptive and unable to establish itself as an autonomous discipline. Although, at the end of the nineteenth century, most biologists saw morphology as "the first evolutionary science" for analyzing and understanding evolutionary changes through time,[11] several scholars argued that it lost this primacy at the beginning of the twentieth century.[12]

This loss of importance is part of a broader historiographical argument that centers on the rise of neo-Darwinism as the valid framework for explaining evolutionary processes. After the first eclipse of his theories,[13] Darwin's insight about the role of natural selection in preserving beneficial modifications would be affirmed by developments in both the emerging field of genetics and the increasing understanding of mathematical population biology, leading ultimately to the establishment of the modern evolutionary synthesis of the 1940s and 1950s. The resulting paradigm—neo-Darwinism—would dominate evolutionary studies for the next fifty years, particularly in the Anglo-American evolutionary community, and would inform further theoretical understandings of the molecular basis of heredity, behavioral evolution (such as altruism and kin selection), macroevolution, and other features of the evolutionary process. By the 1980s, prominent biologists such as Richard Dawkins, Ernst Mayr, John Maynard Smith, and others were prepared to speak of the "triumph" of the neo-Darwinian framework as a complete understanding of the role of natural selection in evolution from the gene to the population. Within this approach to evolution, morphology was viewed as no more than a sort of stamp collecting; as such, its scope was very limited.

As several scholars have compellingly demonstrated, this is only a partial and quite biased chapter of a broader and more complex story. In her seminal book *Biology Takes Form*, historian Lynn Nyhart suggested looking beyond the Haeckel-Gegenbaur school to investigate less prominent figures instead, who contributed significantly, albeit quietly, to the development of morphology. Furthermore, she suggested exploring what happened to scientific zoology during the first half of the twentieth century. As part of this research tradition, "A morphologist was anyone who did not pursue traditional problems organized around systematics, but concentrated instead on problems concerning the 'structure, development

and physiology of animals.'"[14] Last, Nyhart and other scholars questioned the alleged breakdown of morphology during the beginning of the twentieth century. They proposed a continuity of topics between nineteenth-century and twentieth-century morphology instead.[15]

Expanding on these insights, this book examines a morphological tradition, the structural or architectural approach to the form problem, oriented not toward drawing phylogenetic trees but rather to solving evolutionary issues. By doing so, its practitioners were keen to propose the importance of the structural study of form for broadening neo-Darwinian evolutionary mechanisms. This was, in a nutshell, the central idea of the twentieth-century desire for morphology.

The expression "desire for morphology" was coined in 1926. In that year, German pathologist Paul Ernst (1859–1937) gave an influential speech at the Assembly of the German Natural Scientists and Physicians. In his address, Ernst praised Goethe's approach to life sciences and declared that early twentieth-century biology was permeated by a deep desire for morphology. This desire radiated in various biological disciplines and strongly contrasted with a mechanical and quantitative study of organisms. To satisfy this desire for morphology, Ernst proposed a return to Goethe and an organicist approach to biology. In line with Goethe, organic forms must be considered as pertaining "to both what has been brought forth and the process of bringing forth."[16] Furthermore, Ernst noted, morphologists should pursue a "third way" between mechanism and vitalism, given that neither mechanism nor vitalism was the correct approach to grasp and investigate organic form.[17]

Hence, most twentieth-century morphologists sought to understand how organisms were built and how organismal forms could be generated and technically controlled. This was, morphologists believed, essential to understanding the constraints and pathways available to the genetic mechanisms that controlled the evolution of organismal body plans. In short, over the twentieth century, several morphologists looked at the architecture of form and its intrinsic levels of organization and made significant contributions to the field.

This approach to form could not be seen as objections of crackpots or lone dissenters, or as sudden, revolutionary insights, but rather as part of a long, continuous debate about the proper mechanisms and framework with which to understand evolutionary change. In fact, almost all of the practitioners discussed in the following chapters consciously went back to Georges Cuvier (1769–1832), Étienne Geoffroy Saint-Hilaire (1772–1844), Goethe, and other naturalists to show that morphological investigations could be grounded in a myriad of ways. In other words, they strove to show that the Haeckel-Gegenbaur phylogenetic approach to form was neither the only possible way for conducting morphological investigations nor the most fruitful one.

This strategy prompted morphologists to engage with the history of evolutionary morphology. They sought in it a different leitmotif. They searched for a diverse historical path that would open up some room for morphology as an autonomous structural investigation of form development and change through time. For instance, Russian biologist Michael Mikhailovich Nowikoff (1876–1965) emblematically wrote: "It would be very strange if, as in the past, comparative morphology, the science that deals with the most complicated and diverse forms peculiar to living beings, were limited to only one method. According to Hegel's triad principle, Cuvier's thesis must merge with Gegenbaur's antithesis to form a harmonious synthesis. Such a synthesis also facilitates the establishment of a consistent comparative morphology, in which vertebrates as well as the other types of the animal kingdom are discussed side by side."[18] Morphologists were therefore compelled over and over again to reground their discipline. They started this enterprise from scratch every time. They proposed different methods and visualization strategies to ultimately grasp the "riddle of the form."[19] Each chapter of this book presents biologists' need to question and reassess previously accepted methods and eventually establish a new theoretical foundation and a set of practices for morphology.

Although most of these attempts did not lead to any lasting results, two common factors can be identified in the structural study of form. First, the majority of morphologists consciously employed a philosophical language and framework to underpin their methodologies. For instance, Kantian and neo-Kantian philosophy clearly influenced the development of morphological practices and, more broadly, evolutionary biology during the first half of the twentieth century. Further, it is impossible to comprehend the growth of the so-called *Konstruktionsmorphologie* (in either its Tübingen or Frankfurt versions—see chapters 8 and 9) without understanding the philosophical frameworks adopted in this approach. Moreover, morphologists defined form as an emergent property, organism, machine, and so on, and discussed the possible philosophical shortcomings or advantages of these philosophical definitions.

As a result, morphological knowledge production was embedded in a larger and complex philosophical framework. This merger requires a nuanced historical investigation to examine its possible limits, conditions of possibility, and knowledge claims. This book therefore pays particular attention to the rich and substantial intersection between philosophical theories and their implementations in morphological practices. The various philosophical definitions of organic form will become concrete morphological practices and will be situated in the broader history of twentieth-century evolutionary biology.

Second, the use of new technologies like the electron microscope and force plates, as well as tools such as innovative data visualization and the possibility

offered by the introduction of theoretical morphospace (a technique to present all the theoretically possible forms given some parameters—see chapter 7) in the study of form, deeply influenced the development of recent morphology. These technologies did not merely have an auxiliary role. Rather, they coparticipated in the development of morphology and in expanding its theoretical knowledge claims. Furthermore, the supporters of a structural or architectonical approach to form accepted and implemented a technical vocabulary to isolate and study the central factors of organic morphogenesis. This led to the identification of a structural similarity between engineering and evolution as well as to new definitions of organic form. For instance, biologist Hans Petersen (1885–1946) defined form as a "ready-to-use solution to a constructional task" (see chapter 2). As I show in this book, the so-called engineering or constructional approach to evolution brought with it a series of both practical and philosophical problems as well as several epistemic strengths. For instance, and to cite only one merit and one flaw, this approach was burdened with teleological thinking regarding the notion of well-adapted forms. This remained the famous argument from a design developed by English Christian apologist and theologian William Paley (1743–1805) as well as broader reductionistic and materialistic thoughts as expressed by French philosopher La Mettrie (1709–1751), among other radical materialists. At the same time, it also had the virtue of producing a common working language for bringing together biologists, architects, and engineers.

These two factors were based on a broader tenet: *morphological knowledge production was possible only through knowledge circulation*. As the following chapters amply illustrate, architects, engineers, biologists, paleontologists, and artists communicated in all sorts of ways to grasp the origin of organic form. A particularly important synthesis was D'Arcy Thompson's book *On Growth and Form*, published in two editions in 1917 and 1942. In it, Thompson attempted to deal with form in a "very concrete way," as "a quasi-mechanical effect on Matter of the operation of chemico-physical forces."[20] By defending an architectonical approach to form and evolution (form as a result of material proprieties and physical and chemical constants), Thompson's book catalyzed the interest of several biologists and architects, thus paving the way for a renaissance of the science of form.

Hence, as this book argues, the history of twentieth-century morphology is first and foremost a history of the interactions between artifacts and organisms (their similarities and differences) and, therefore, a history of the interconnections among technology, life, material cultures, art, and science: it is an entangled and cross-disciplinary history of knowledge production and circulation. In fact, one notable feature of this development was a concerted effort by morphologists

to reach outside of the biological community for sources of engagement and inspiration: by exchanging their data, knowledge, and practices with architects and engineers (such as Richard Buckminster Fuller, Pier Luigi Nervi, György Kepes, Frei Otto, and others), morphologists abandoned a naive organism-machine analogy and focused instead on the notion of form as "construction." As a result, morphologists like D'Arcy Thompson, Adolf Seilacher, Carl Pantin, Lancelot Law Whyte, Stephen Jay Gould, and others developed and reinterpreted important notions, such as constraints, modularity, *Bauplan*, ontogenesis, and organism, that would play a central role in the late 1980s development of evolutionary developmental biology (evo-devo). The interaction between biologists, architects, and engineers should not be seen only as a one-way direction. Architects and engineers also approached biologists to investigate the enigma of organic form and develop design principles together.

The strong connection between architecture, engineering, and evolutionary morphology is certainly not the hallmark of only twentieth-century science. Encounters between these disciplines characterized the entire history of design—see, among others, the radiolarian-inspired pavilion at the 1900 Paris world's fair or Haeckel's influence on *Jugendstil*.[21] What is new though is that, in the twentieth century, (1) long-standing research centers were established to provide the necessary infrastructure and financial support to allow knowledge to flow from biology to architecture and vice versa over decades, and (2) designers and biologists concretely worked together to investigate bottom-up form-finding processes. It is important to note that the circulation of knowledge between biologists, architects, engineers, and vice versa was a concrete activity. Besides reading, quoting, and citing one another, the scientists interested in form's structural elements organized conferences, coauthored papers, popularized their approach through museum exhibitions, and embarked on joint research groups: they constantly and actively networked and cooperated with one another.

In order to offer this rich development and to provide an expanded history of twentieth-century science of form, I present an additional picture of knowledge exchange. This book goes beyond a binary history of science in which, for instance, the conflicts between quantitative and qualitative methods, descriptive and experimental science approaches, field and laboratory spaces, and mainstream and outsider scientists guide the narrative. This binary opposition has characterized the historiography of morphology and twentieth-century science for several decades. But, if we shift our focus and analyze how knowledge circulated between different cultures (to, for example, Western and Eastern contexts), between different political, social, and philosophical systems (for example, between romantic biology and neo-positivistic philosophy), and between biological

and nonbiological disciplines (for instance, between evolutionary biology, architecture, and engineering), new layers of nuance can be added to understanding the role of morphology in twentieth-century science. Thus, this book examines how morphological knowledge was established and traveled[22] by investigating the work of morphologists in their local environments as well as the transnational activities and impacts of morphological thought and research.

Hence, by examining how this circulation and transfer of practices and technology took place, my book pushes the history of a scientific discipline, morphology, toward a broader philosophically informed and cross-disciplinarily engaged history of knowledge.[23] This will bring the history and philosophy of science closer to the history and philosophy of knowledge. In fact, one of the main features of twentieth-century morphology is that it is situated in between disciplinary boundaries. Over the course of the twentieth century, morphological knowledge became what I like to call interstitial knowledge. That is, it became a transition point between biological and technical disciplines. From time to time, practitioners attempted to transform this interstitial complex of knowledge into an autonomous site of knowledge production. However, as happens with interstitial spaces in architecture, such as in spaces located between existing buildings or regularly accessible floors, the study of form eventually remained a crossroads and transition point open to be taken up, rejected, expanded, constrained, and redesigned in response to practitioners' diverse needs and modalities.

Although the book follows a chronological order of events (from the early twentieth century to the Dahlem meeting on evolution and development in 1981), each chapter's narrative is framed by specific problems, concepts, and approaches to morphology. This strategy enables a transversal glance at how morphological knowledge and practices traveled between different national contexts and disciplines.

Chapter 1 sets the scene. After outlining the debate between vitalist and mechanist biologists on the correct study of form, I will focus on a first attempted escape route from this metaphysical debate. This was conceived by Scottish polymath D'Arcy Thompson.

Chapter 2 explores an approach to the morphological problem strongly rooted in the engineering and philosophical reflection of the first decades of the twentieth century. In particular, it deals with the practices developed by several German-speaking biologists who opposed an abstract notion of *machine* used by the majority of biologists. Conversely, they equated organic form with construction.

Chapter 3 deals with the study of the architecture of the organism. In the first decades of the twentieth century, a group of biologists networked to study the phenomena of biological parallelism and the notion of analogy.

Chapter 4 continues the analysis of the clash between biologists who supported the independence of morphology from genetic explanation and the supporters of the modern synthesis of evolution. It illustrates two different models of synthesis. On the one hand, the English-speaking modern synthesis of evolution granted morphology no independent space. On the other hand, in the so-called biological synthesis carried out in German-speaking countries, morphology was set as an independent and important discipline.

Chapter 5 investigates post–World War II morphology by looking at three exhibitions and workshops organized in 1951. This chapter illustrates how evolutionary morphology started to become an interdisciplinary field of inquiry.

Chapter 6 analyzes Anglophone morphological research during the 1960s and early 1970s. It explores the quite innovative investigations conducted by different biologists in the UK and the USA.

In chapter 7, I analyze a peculiar engineering-based approach to form, which American paleontologist Stephen Jay Gould defined as "quantificational." Ironically, Gould himself championed the denunciation of this approach to morphology.

Chapter 8 investigates one of the major reasons that prompted Gould to change his mind on the quantificational approach to form: his encounter with German-speaking morphological tradition during a workshop in 1971. Particularly, Gould's admiration for German paleontologist Adolf Seilacher's Konstruktionsmorphologie.

Almost entirely based on archival sources, chapter 9 explores the development of German-speaking morphology throughout the 1970s. Specifically, it analyzes a different version of Konstruktionsmorphologie established in Frankfurt by German biologist Wolfgang Friedrich Gutmann (1935–1997).

The tenth and concluding chapter illustrates how the structural approach to form developed in German-speaking countries entered into mainstream Anglophone evolutionary research. In the book epilogue, I reflect on the broader features of twenty-first-century morphology and on the notion of knowledge circulation and production.