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THEMATIC ISSUE ARTICLE: D'ARCY THOMPSON'S CONCEPTUAL LEGACY

From the Method of Division to the Theory of Transformations: Thompson After Aristotle, and Aristotle After Thompson

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Abstract

Aristotle's influence on D'Arcy Thompson was praised by Thompson himself and has been recognized by others in various respects, including the aesthetic and normative dimensions of biology, and the multicausal explanation of living forms. This article focuses on the relatedness of organic forms, one of the core problems addressed by both Aristotle's *History of Animals* (*HA*), and the renowned chapter of Thompson's *On Growth and Form* (*G&F*), "On the Theory of Transformations, or the Comparison of Related Forms." We contend that, far from being an incidental inspiration stemming from Thompson's classicist background, his translation of *HA* played a pivotal role in developing his theory of transformations. Furthermore, we argue that Thompson's interpretation of the Aristotelian method of comparison challenges the prevailing view of Aristotle as the founder of "typological essentialism," and is a key episode in the revision of this narrative. Thompson understood that the method Aristotle used in *HA* to compare animal forms is better comprehended as a "method of transformations," leading to a morphological arrangement of animal diversity, as opposed to a taxonomical classification. Finally, we examine how this approach to the relatedness of forms lay the foundation for a causal understanding of parts and their interconnections. Although Aristotle and Thompson emphasized distinct types of causes, we contend that they both differ in a fundamental sense from the one introduced by Darwin's theory of natural selection, which was formulated as a solution to the species problem rather than the form problem. We conclude that Thompson's interpretation of Aristotle's approach to form comparison has not only impacted contemporary scholarship on Aristotle's biology, but revitalized a perspective that has regained significance due to the resurgence of the problem of form in evo-devo.

Keywords Aristotle · Evo-devo · Morphology · Taxonomy · Theory of Transformations · D'Arcy Thompson

D'Arcy Thompson: The Scholar-Naturalist

D'Arcy Thompson is widely regarded as one of the last exemplars of Renaissance men. His daughter, Ruth D'Arcy Thompson, entitled the biography of her father *D'Arcy Thompson: the Scholar-Naturalist* (1958), stressing the inseparability of his two passions, as expressed in this quote from his address to the Classical Association of Cardiff:

> Science and the Classics is my theme today; it could hardly be otherwise. For all I know, and do, and well nigh all I love and care for (outside of home and friends) lies within one or the other; and the fact that I have loved them both has colored all my life, and enlarged my curiosity and multiplied my inlets to happiness. (Thompson 1940, p. 2)

Thompson was not an amateur, but a recognized scholar of Greek and Latin classics, especially of ancient Greek zoological works: *A Glossary of Greek Birds* (1895) and *A Glossary of Greek Fishes* (1947) trace the natural history of these animals throughout ancient literature. In particular, Thompson was an enthusiast of Aristotle's biological treatises. When he was elected to the Cambridge Natural Science Club in 1881, he read his first paper on Aristotle's scientific works, a subject that became a lifelong interest. In 1910, Thompson published his translation of Aristotle's *History of Animals*, an immense task on which he had intermittently worked for many years. In 1913, he gave his magisterial Spencer Lecture, "On Aristotle as a Biologist" (1913), and

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his magnum opus, *On Growth and Form* (1917), accurately described by Stephen Jay Gould as "a work of natural philosophy" that synthesized his two lives as a classicist and zoologist (Gould 1971, p. 236), makes recurrent references to Aristotle. After the publication of *On Growth and Form*, Thompson wrote two more essays on Aristotle: one later reprinted with the title "Aristotle as a Naturalist" ([1921] 1940), and an article in the journal *Mind* on the notions of "excess and defect" and "the more and the less," and Aristotle's use of them in his zoology (1929).

Thompson's admiration for the ancients has been interpreted differently based on various conceptions of the history of science, from being dismissed as a relic perpetrating inadequate science, to being praised for its "ability to bring new ways of thinking to an old problem" (Gould 1971, p. 249). Aristotle's influence on Thompson's understanding of organic form was recognized by Thompson himself and has been emphasized in various aspects, encompassing the aesthetic and value dimensions of studying living nature, as well as the explanation of biological organization arising from multiple intertwined causes (Gould 1971; Kemp 2011). This article focuses on the relatedness of organic forms as a problem addressed by both the *History of Animals HA* and the most famous chapter of *On Growth and Form* (*G&F)*, "On the Theory of Transformations, or the Comparison of Related Forms." We contend that, far from being an anecdotal inspiration embedded in Thompson's classicist background, the translation of *HA* (Thompson 1910) played an instrumental role in developing his method of coordinate grid transformations. Moreover, we argue that Thompson's interpretation of the Aristotelian method of division as a morphological method contradicts the received view of Aristotle as the founder of "typological essentialism," a philosophical tradition that, as defined by the historians and philosophers of the Modern Synthesis, would be the core hindrance not only to evolutionism but more generally, to scientific progress. There is no doubt that Aristotle was an essentialist, but not, we will argue, of this kind.

In the last few decades, the so-called "essentialism story" (Amundson 2005; Winsor 2006b) has been challenged on many historical and philosophical grounds. We argue that Thompson's translation of *HA* (Thompson 1910) and his interpretation of the Aristotelian method of division in *G&F* are key episodes in the revision of this narrative. Firstly, Thompson realized that in order to understand the epistemic goals of *HA*, it was essential to understand Aristotle's discrimination between the description and the explanation of organismal form, a fundamental distinction that guided his own project. Secondly, Thompson recognized that *HA* was not primarily a taxonomic work for classifying species, but a theoretical treatise aimed at organizing information about animal form. Aristotle's definitions encompass the essential features of animal kinds, often functional features that explain their structural attributes. To identify these explanatory essential features, Aristotle employs a method of transformations that anticipates the comparative method of morphology. Furthermore, Thompson also noticed that the study of morphological correlations played a crucial role in Aristotle's integrative approach to animal diversity. Finally, *G&F* develops a major implication of Aristotle's biological work, namely that the study of the relatedness of parts and of their combinatorial logic opens the way for a theoretical morphology. We conclude that Thompson's approach to "The Comparison of Related Forms" rests on a highly original reading of *HA*. In turn, we demonstrate how this interpretation has influenced contemporary scholarship on Aristotle's study of animal diversity, as well as recent affirmations of the significance of his philosophy for contemporary evolutionary biology. D'Arcy Thompson's interpretation of Aristotle's approach to form comparison as a method for studying morphological transformations revitalizes a perspective that was overshadowed by neo-Darwinism, but has regained significance due to the resurgence of the problem of form in evo-devo. More generally, this episode in the history of comparative biology shows the importance of conceptual phylogenies for the understanding of present science (Lennox 2001), and demonstrates the fruitful interaction between science and the classics (Thompson 1940).

D'Arcy Thompson on Aristotle as a Biologist

While Aristotle's biological treatises were still regarded by many in the 1950s as a curiosity pervaded by empirical errors, D'Arcy Thompson was a forerunner in arguing for the importance of biology for understanding Aristotle's philosophy. Thompson's vision was a product of his double nature as a classicist and as a biologist. The greatest 19th-century comparative anatomists, including Étienne Geoffroy Saint-Hilaire (see below), Georges Cuvier (Pellegrin 1982), Richard Owen (Camardi 2001), and Darwin himself (Gotthelf 1987) were all impressed by Aristotle's biology, and none regarded it as an instantiation of the typological essentialism depicted by historians and philosophers of the Modern Synthesis. Thompson was, in turn, a passionate reader of this literature, and shared with it an understanding of the embedded philosophy deployed in Aristotle's biological treatises.

Thompson's belief in the importance of biology in Aristotle's philosophy was based on two core, related arguments: the quality and extent of Aristotle's zoological knowledge and the time in which Aristotle acquired such knowledge, which, in Thompson's view, preceded his later metaphysical works. Both arguments were neglected during a good deal of the 20th century, and only in the late 1980s came to be a consensus interpretation among Aristotle scholars (see Lennox and Gotthelf 1987). In turn, the recency of this consensus might partly explain the Whiggish, erroneous interpretation of Aristotle's philosophy among philosophers and historians of biology forged in the frame of the Modern Synthesis.

On the one hand, D'Arcy Thompson was fascinated by Aristotle's zoological knowledge. In his Spencer lecture, Thompson distinguishes two ways of reflecting on Aristotle's biological treatises: one needs "either to deal with Aristotle's theories or his facts, his insight or his erudition" (1913, p. 17). Because of space constraints, he decides to confine himself to the latter and devotes the core of his lecture to discussing "a few fragments out of his storehouse of zoological and embryological facts" (1913, p. 17). After analyzing these fragments, Thompson argues that one cannot explain the accuracy of Aristotle's descriptions by assuming that he depended on the reports of fishermen. Instead, they "could only have been made by a skilled and learned anatomist" (1913, p. 22). In commenting on Aristotle's description of the anatomy, habits, and development of mollusks, he writes that far from being "a mass of fragmentary information gleaned from the fishermen," it is "a plain orderly treatise" that found no comparable project until Cuvier (1913, p. 19). Thompson then goes on to discuss Aristotle's descriptions of fishes, and again, he finds "fishes that have only recently been rediscovered," "structures only lately reinvestigated," and "habits only of late made known" (1913, p. 18). In commenting on Aristotle's discovery of placental viviparity in some species of sharks, he writes again that this discovery requires the expertise of a skilled anatomist[1] (1913, p. 21). This also applies to Aristotle's mistakes: when he attributed to the heart a central role in the organization of blooded animals, it was based on the observation of its early development in the chick: "Right or wrong, it was on observation, and on his rarer use of experiment, that Aristotle relied" (1913, p. 21). In his later essay on "Aristotle as a Naturalist," Thompson considers Aristotle to be the founder of biology as a science, deserving the same merit as Pythagoras for mathematics, or Boyle for chemistry:

> There was a wealth of natural history before his time; but it belonged to the farmer, the huntsman, and the fisherman—with something over (doubtless) for the schoolboy, the idler, and the poet. But Aristotle made it a science, and won a place for it in Philosophy. (1921, p. 143)

And just as the Pythagorean theorem or Boyle's law belong to modern mathematics and modern chemistry, Aristotle's biology is "our" biology. In a conclusion worth quoting at length, Thompson makes the point forcefully:

> When he writes upon Mechanics or on Physics we read him with difficulty: his ways are not our ways; his explanations seem laboured; his science has an archaic look, as it were coming from another world to ours, a world before Galileo. Speaking with all diffidence, I have my doubts as to his mathematics…. But he was, and is, a very great naturalist. When he treats of Natural History, his language is our language, and his methods and his problems are well nigh identical with our own. He had familiar knowledge of a thousand varied forms of life, of bird and beast, and plant and creeping thing. He was careful to note their least details of outward structure, and curious to probe by dissection into their parts within. He studied the metamorphoses of gnat and butterfly, and opened the bird's egg to find the mystery of incipient life in the embryo chick. He recognized great problems of biology that are still ours to-day, problems of heredity, of sex, of nutrition and growth, of adaptation, of the struggle for existence, of the orderly sequence of Nature's plan. (1921, p. 143)

On the other hand, in this lecture, Thompson argues for the temporal and conceptual priority of Aristotle's biological treatises with regard to his metaphysical works, an issue he had already referred to in the Prefatory Note of his translation of *HA* (Thompson 1910, p. vii) and to which he later returned (Thompson 1921). After discussing the geographical location of many of the species discussed in his biological treatises, Thompson concludes that it is very likely "that an important part of Aristotle's work in natural history was done upon the Asiatic coast, and in and near to Mitylene" (Thompson 1913, p. 13). This fact has—according to Thompson—two important consequences. First, it corroborates his view of Aristotle as a skilled anatomist: Aristotle did not just collect information from his conversations with fishermen, but he really "loved and knew" all the creatures he described. A recent comprehensive examination of Aristotle's mentions of dissections by Lennox (2018) substantiates Thompson's assertion on this matter. Second, Aristotle's biological investigations preceded his more strictly philosophical endeavors. Recognizing this chronological sequence is crucial when considering the impact of his biology on his philosophy. Thompson's interpretation

[1] These remarks of Thompson's are admittedly speculative. Aristotle's description is vague, and it is not clear which species he is referring to. See Thompson's notes 5, 6 to *HA* 565a23-28 and note 1 to 565b6 (Thompson 1910).

has come to be the chronological scenario assumed as most likely by contemporary scholars. It is now widely accepted that his biological treatises "are not just empirical studies in which some philosophical concepts are put to use." Instead, "there is a reciprocal influence between the biological and metaphysical treatises" (Balme 1987a, p. 18). But this was not always the case. Jaeger's theory (1948; see also Nuyens 1948) was that Aristotle did his biological studies in the Lyceum after completing his philosophical work. In his essay on "The place of biology in Aristotle's philosophy," David Balme accuses this interpretation of "forcing chronology to match an imaginary intellectual progress" (Balme 1987a, p. 12). Balme then refers to Thompson's preface to his translation of *HA*, followed and confirmed by the thorough analysis of place names by Lee (1948). Only then, "most scholars, accepted this dating" (Balme 1987a, p. 13).[2] Again, far from being a curiosity for biographers, the chronological and conceptual relationship between the biological and the logical and metaphysical treatises has crucial consequences for understanding Aristotle's philosophy, and Thompson's awareness of this fact gives us an idea of how he read and translated Aristotle's zoological works, and how this interpretation affected his parallel conception of *G&F*.

D'Arcy Thompson as an Aristotelian: Two Theories of Form

Despite Thompson's profound interest in Aristotle as a biologist, commentators have often overlooked his influence on Thompson's own scientific work. In his essay "D'Arcy Thompson and the Science of Form," Gould argues that, "Aristotle represented only one of the two classical inputs to D'Arcy Thompson's science—and the one of lesser importance for *Growth and Form*…. It is to Pythagoras and the later Plato of the *Timaeus* that D'Arcy Thompson owes his vision" (Gould 1971, p. 236). According to Gould, Thompson "revered Aristotle as a descriptive naturalist," but "identified as Aristotle's weakness what most critics consider the twin strengths of *Growth and Form*: aesthetic style and mathematical skill" (Gould 1971, p. 239). Gould acknowledges that Thompson's perspective on mathematics shared crucial aspects with Aristotle's, such as "the essential embeddedness of mathematics in the fabric of things" and the dynamic nature of organismal form. However, when it comes to the theory of transformations, Gould, among others, either interprets it as a Platonic endeavor seeking to relate pure form to abstract geometry, or as a first approximation of a physical explanation.

This is not surprising. Despite the fact that, as we will argue in the following section, Thompson correctly read the first four books of the *History of Animals* as a treatise in comparative anatomy, the prevalent interpretation was that it was a failed taxonomy.[3] This became the mainstream view among historians of biology in the 20th century, who considered Aristotle's method for relating animals to be the one used by Linnaeus in his systematics, thus founding the taxonomical tradition associated with essentialism and fixism (Cain 1958; Ereshefsky 2001; for critical assessments of the "essentialism story," see Amundson 2005; Winsor 2006a; Lennox 2017b). In an influential paper, Hull (1965) defined typology as the instantiation of "essentialism" in taxonomy, and accused it of being responsible for taxonomy becoming the last discipline to experience the scientific revolution. Karl Popper had previously defined essentialism as a philosophical tradition according to which the goal of science is to define the essence of things by means of necessary and sufficient properties, charging the Aristotelian method of definition with being the main hindrance to scientific progress throughout history (Popper 1945, p. 206). Influenced by Popper, Hull (1965) argues that this was also the case for the history of taxonomy, and locates in Aristotle's method of definition the reason for what he calls the "stasis" of taxonomy. According to this perspective, until the advent of evolutionary systematics, taxonomists were unable to define species in the right way because they did not get rid of the Aristotelian method of definition. Contrary to the entities of physics and chemistry, which (ruled by laws) can be grouped into universal classes, species are historical individuals whose features can change throughout evolutionary time without losing their individuality: only individuals, not classes, can evolve.

According to the essentialism story, Aristotle inherited Plato's method of division and applied it to the classification of natural-historical data in his zoological treatises, particularly in the *History of Animals*. In this view, Aristotle was engaged in the project of classifying animals into a hierarchy of genera and species by virtue of their essential properties. A species definition would give its essence, understood as a list of properties that are necessary to be a member of a genus, and a subset of these properties that differentiate

[2] A related controversy Thompson didn't comment on concerns the chronological and conceptual relationship of *HA* and the other biological treatises. Balme argued that, "*HA* was written by Aristotle during and following his stay on Lesbos, and after writing the other biological treatises" (Balme 1987a, p. 17). Lennox (1996) has noted that one needs to distinguish when and where research was done from when and where treatises were written. Moreover, even if *HA* was written after the *Parts of Animals* and *Generation of Animals*, the research there recorded corresponds to the preliminary stages of inquiry according to Aristotle *HA* 491a7-15).

[3] Moreover, in the 1960s the problem of form got dissolved in the framework of the Modern Synthesis, either by conflating it with that of adaptation, or by reducing it to the classification or the systematic description of diversity.

it from other species within this genus. As a consequence, Aristotle's organization of animal diversity is interpreted as a hierarchical and dichotomous system (Ereshefsky 2001, p. 20). In turn, Linnaeus would have inherited the method of division from Aristotelian scholasticism and adapted it to the classification of species, as illustrated by his sexual system of plants (Cain 1958; Ereshefsky 2001). As reported by the standard view, the classification of species by the method of logical division entailed the definition of the essence of the entities constituting the taxonomic system. However, recent research by historians of taxonomy challenges the notion that essentialism and Linnaean systematics were closely linked (Winsor 2006a; Müller-Wille 2011; Richards 2010; Wilkins 2011). The primary goal of 18th-century systematics was to organize natural-historical data and identify species, rather than defining their essences through logical division. Alternative, inductive methods were increasingly employed during this period to describe species, indicating that the ontological debate on the essence of species did not dictate taxonomic practices. Moreover, pre-Darwinian naturalists adopted different criteria for defining species, rather than relying solely on essential properties, an approach that Linnaeus himself considered artificial. Therefore, what Darwin faced was not Aristotelian essentialism or the "typological species concept," but rather the species problem arising from the diverse and conflicting criteria used to identify species (Richards 2010; Wilkins 2011; Lennox 2017b).[4]

Although originally used with reference to taxonomy, Mayr later generalized the dichotomy between population and typological thinking from taxonomy to biology in general (Chung 2003; Witteveen 2015, 2016). Morphology was one of the main disciplines to suffer from this generalization, and it was argued that it was excluded from the Evolutionary Synthesis for good reasons: the emphasis on the unity of type entailed a disregard for variation that was incompatible with modern evolutionary thought (Coleman 1998). However, since the 1980s morphology has experienced a renaissance in evolutionary biology, entailing the return of typological concepts such as "type," "archetype," "morphotype," "Bauplan," and "homology" (Wagner 1996; Rieppel 2006). In this context, philosophers have reconsidered the epistemological and ontological status of typology (Amundson 1998; Brigandt 2007; Love 2009), and historians have challenged the received view of key episodes in the history of morphology, distinguishing typology from the metaphysical commitments associated with essentialism (Amundson 2005).

Independently of the interpretation of the status of types in pre-evolutionary morphology, what needs to be emphasized for the purposes of this article is that the explanandum of morphology was not that of taxonomy: the problem of morphology was not the species problem, but the problem of form. Morphologists were not interested in taxa but in structures. As a consequence, the notion of type does not apply to species, but to structures shared by wider taxonomic groups (Russell 1916, p. 81). In this sense, and contrary to the received view, the morphological type concept denies the individuality of species (Amundson 1998). The goal of morphology is not to describe and classify into categories animal diversity, but to establish the relatedness of organic forms and to understand the logic of morphological variation. In morphology, two forms belong to the same type if one form can be transformed into the other. In the words of Goethe, morphology aimed at "establishing the rules of transformation through which nature can produce the most varied forms by modifying one unique organ" (1995, p. 76).

In the next section, we will argue that the Aristotelian study of animal form was a morphological endeavor. As scholars of Aristotle's biology have shown in the last few decades, neither the epistemic purposes nor the methodology used in *HA* are related to the goals and methods of taxonomy. The essentialism story forged by neo-Darwinians neglected Aristotle's actual philosophy of biology (Lennox 2017b) and was based on the taxonomical reinterpretation of the method of division by someone (Linnaeus) who, in turn, never cited Aristotle (Müller-Wille 2007). Instead, when applied to the shape and structure of body parts, *HA* should be interpreted, not as a proto-taxonomy, but as a proto-morphology.[5] As detailed in "The Explanation of Form" section, Aristotle's perspective on organismal form transcends mere geometry or topology; instead, it is fundamentally rooted in the vital, functional dimension interwoven with the individual organism's conditions of existence, as Thompson was well aware:

> Above all he [Aristotle] was a student of Life itself. If he was a learned anatomist, a great student of the dead, still more was he a lover of the living. Evermore his world is in movement. The seed is growing, the heart beating, the frame breathing. The ways and habits of living things must be known: how they work and play, love and hate, feed and procreate, rear and tend

[4] The independence between the definition and the identification of species implies that essentialism and fixism were not intrinsically linked, as shown by the fact that Linnaeus himself speculated on the evolution of new species through hybridization among genera.

[5] As indicated above, Aristotle applies the method of the more and the less not only to parts, but also to activities. In several books of *HA* dealing with methods and processes associated with successful reproduction (books V, VI, and IX), Aristotle discusses reproductive organs in forms of various kinds, but much of what we find in these books, as well as books VII and VIII, is about animal behavior in relationship to their environments. These books might be interpreted as a proto-ethology and a proto-ecology more than as a proto-morphology.

> their young; whether they dwell solitary, or in more and more organized companies and societies. All such things appeal to his imagination and his diligence. Even his anatomy becomes at once an *anatomia animata*, as Haller, poet and physiologist, described the science to which he gave the name of physiology. This attitude towards life, and the knowledge got thereby, afterwards helped to shape and mould Aristotle's philosophy. (1921, p. 143)

Yet, the priority of function does not preclude its separation from structure, two aspects of living form frequently conflated in the history of biology (Minelli 2021). Aristotle's achievement lay in precisely delineating criteria for their conceptual differentiation, enabling comparisons of body parts based on both shape and topology, followed by explanations grounded in their function and development. Our assertion is that the method introduced in the first four books of *HA* to compare animal parts is better comprehended as a "method of transformations," leading to a morphological arrangement of animal diversity, as opposed to a taxonomical classification. Thompson's translation of *HA* (Thompson 1910), along with his mathematical reinterpretation of the Aristotelian method in the 17th chapter of *G&F*, are key episodes in enabling this interpretation.

The Method of Division as a Method of Transformations

We have seen that the prevalent interpretation of Aristotle's (*HA*) was that it was a preliminary attempt to classify animals by the method of division that was later systematized by Linnaeus. Yet, despite the attempts to interpret the notions of γένος (*genos)* and εἴδος (*eidos*) within a taxonomical framework, the use of these terms in Aristotle's biological treatises was hard to understand from a taxonomical perspective. In some texts, Aristotle does indeed appear to use the terms "eidos" and "genos" as taxonomical categories, with meanings similar to our modern "species" and "genus." But on many other occasions, these terms are used in such a contradictory way (if looked at from the viewpoint of taxonomy) that scholars never agreed upon the details of Aristotle's alleged classifications (Balme 1987b). Thompson himself vacillated in his use of these terms in his translation. Sometimes he translates εἴδος as "species" (486a19) while in a nearby passage, he translates it as "form" (486b18). With γένος he most often uses "genus," but on some occasions, he translates it as "kind" (487b9), as "genus" of a "kind" (490b9-10), or even as "race" (488a30) or "tribe" (488b5).[6] This flexibility in the translation of the terms εἴδος and γένος shows that Thompson was well aware that these terms could not refer to fixed taxonomic categories, as he later made explicit in his essay on Aristotle's natural science: "Many commentators have sought for Aristotle's 'classification of animals'; for my part, I have never found it, and, in our sense of the word, I am certain it is not there" (1921, p. 158).

During the first half of the 20th century, Aristotle scholars vacillated in the interpretation of the apparent contradictions in the use of these terms. Some interpreters concluded that Aristotle simply had failed in applying his logical method to the irreducible diversity of animal forms, while others saw the *HA* as a poorly organized zoological notebook where he had collected natural-historical data that would later be the subject of causal exploration.[7] However, since Balme's seminal paper on Aristotle's method of division (Balme 1962), scholars have come to agree that the paradoxes of the *HA* should not be ignored or interpreted as a failure (Lennox 1980, 1989; Pellegrin 1982, 1987; Balme 1987b). Instead, contradictions vanish once one recognizes that Aristotle was committed to an entirely different project. As Thompson believed, "Aristotle's aim was not taxonomy" (Balme 1987b, p. 84). The goal of *HA* was not to classify but to investigate the many ways in which animals differ—their parts, their habits and activities, and their ways of life (Balme 1962, 1987b; Lennox 1987). Importantly, this goal is subordinated to the ultimate goal of *explaining* this diversity. The systematic study of the differences and attributes of animals accomplished in *HA* is the first stage in the pursuit of causal explanations (*HA* I 6, 491a9-11) which are addressed in the other zoological treatises, such as *Parts of Animals* (*PA*; Lennox 2002), and *Generation of Animals* (*GA*). As we will argue in the next section, understanding the method Aristotle used to pursue the preliminary goal of organizing animal diversity is essential to understanding his explanatory project.

The method of division was introduced by Plato as a procedure for reaching a definition by which a general group (*genos*) is continually divided into smaller groups (*eidos*) until the definition is reached. However, the terms *genos* and *eidos* do not mark a fixed level of generality. Instead, the subordination of *eidos* to *genos* is not absolute but relative.

[6] For example, Thompson translates 490b9-10 as follows: "There is another genus of the hard-shelled kind, which is called oyster; another of the soft-shelled kind." In this passage, "another genus" translates ἄλλο γένος, whereas "the hard-shelled kind" translates τὸ τῶν ὀστρακοδέρμων [γένος] and "the soft-shelled kind" τὸ τῶν μαλακοστράκων [γὲνος]. In these two cases, γένος must be supplied, but it is the obvious complement for τὸ in both cases.

[7] For details, see the introduction to Peck's (1965) translation of *HA* I-III, pp. v-xxxii.

Every *eidos* can, in turn, be taken as a *genos* until the division reaches the last indivisible *eidos*. For example,

> we might divide animals into tame and wild, then the tame into gregarious and solitary, the gregarious into aquatic and terrestrial, the terrestrial into horned and hornless, and so on until we narrow it down to a class which contains only our definiendum. Then by recalling all the divisions we can show the forms in which it participates—it is animal, tame, gregarious, terrestrial, hornless, etc. (Balme 1987b, p. 70)

Hence, *genos* and *eidos* are relative concepts that cannot be translated as fixed taxonomic categories (see also Lennox 1980, 1987; Pellegrin 1982).

Aristotle inherits Plato's method of division as a method of definition, not as an instrument of classification, but he introduces major innovations in the use of the method that radically move him away from his master's way of understanding beings, in particular living beings (*PA* I.2–4; see Balme 1987b). Firstly, each animal kind cannot be defined by a single line of differentiation, but needs to be "defined by many differences" (*PA* I.3, 643b12-13), that is, by multiple traits concerning their parts, their reproductive behavior, their activities, their characters, and their ways of life. Secondly concerning the way to characterize each of those differences, Aristotle confronts Plato's dichotomous and arbitrary method: instead, he recommends that division proceeds by successive differentiation, intended to preserve the unity of definition. For example, "footed" can be differentiated as quadruped or biped, but not as gregarious and solitary, because the latter are not sorts of footedness. Thus, in Aristotle "*[d]ifferentia* comes to connote determination as well as discrimination, shaping as well as sorting" (Furth 1987, p. 51) and moves from its older association with ideas like "dividing" kinds, toward something more like an "articulation" of a typical structure in a typical organism. Hence, *genos* refers to relatively undetermined or generically characterized structures which are successively determined or specified, whereby the *differentiae* are the particular ways in which that generic potentiality is restricted (Pellegrin 1987, p. 322). In this sense, the *genos* is analogous to the morphological type concept, an abstract model that captures the extent and the limits of the variations a given form can express. The variations distinguishing the *eidê* of a *genos* are "more and less" differences, that is, continuous differences along multiple axes (Lennox 1980): for example, when birds are compared, it will be observed that they differ "by means of excess or deficiency of their parts, and according to the more and less. That is, some of them are long-legged, some short-legged, some have a broad tongue, others a narrow one, and likewise too with the other parts" (*PA* IV.692B3-7). By contrast, when birds are compared with fishes, it will be observed that they differ "by analogy": that is as lungs are to birds, so gills are to fishes; as scales are to fishes, so feathers are to birds.

As Thompson is well aware, Aristotle borrows the expressions "more and less" or "excess and defect" like *analogon*, from mathematical practice. Under this framework, some scholars prefer to translate "genus" and "species" as "kind" and "form," respectively (Lennox 2017b). The reason is that contrary to taxonomical categories, *genos* and *eidos* are not extensional concepts devoted to classifying, but to defining objects: the *genos* acts as the material substrate that, through the method of the more and the less, is differentiated into different *eidê*. Importantly, Aristotle not only applies this method to anatomical parts but also to activities and ways of life, as he makes clear in his introduction to book VIII of *HA*. However, in *G&F*, Thompson only applies it to anatomical shape, where a geometrical method of transformations can be readily used and visualized. Furthermore, even when applied to parts one major difference between Aristotle's and Thompson's technique is that for Aristotle the more and less differences include differences in texture (hardness and softness), color, and other qualitative differences which could not be easily mapped and transformed on a Cartesian grid. In this regard, Thompson's stress on shape is more limited in application than Aristotle's, given that Aristotle's requires variations along many more than the three spatial dimensions. But in a more fundamental sense, Thompson's and Aristotle's methods share the same goal: neither of them is addressed to measure variation (in shape or in other qualitative features) but to understand the logic of this variation. As Fred Bookstein pointed out in his article on Thompson's method, "[h]is goal was not to measure: he was content to exemplify the geometry logically prior to any measure" (Bookstein 1977, p. 196). Thompson's deformation grids were a key influence in the foundation, a decade later, of geometric morphometrics, the statistical analysis of shape-based landmark coordinates (see Bookstein 1998; and Mitteroecker and Gunz 2009 for historical reviews). In 1982 Bookstein depicted the Cartesian method of transformations as the "fundamental construct of morphometrics," where "a mathematical object, i.e., a deformation, is used to represent explicitly the relation of a pair of forms" (1982, pp. 452-453). Bookstein proceeds to categorize the comparison of shape based on sets of landmarks as "another version" of the same interplay between geometric location and biological homology (1982, p. 453). The fundamental nature of the approach initiated by Aristotle, subsequently advanced by Thompson and later by Bookstein and the whole field of geometric morphometrics harmonizes with the broader relationship between meaning and measurement in biological theory (Houle et al. 2011). Viewed from this standpoint, the evolution of scientific concepts can be understood as a transition from verbal models to quantification. This episode distinctly exemplifies such a shift, starting with Aristotle's verbal model of the more and the less, progressing through Thompson's visual methodology, and culminating in the computational analysis of organismal shape in geometric morphometrics. Thompson himself viewed it this way (1917, pp. 719–720), although, as we will elaborate in our final section, his ultimate objective wasn't measurement but dynamic explanation grounded in physical forces.

Aristotle's method was recognized by the founders of pure morphology as the pioneer method in organizing animal diversity in a morphological way. In his "Preliminary Discourse" to the second volume of *Philosophical Anatomy*, Geoffroy Saint Hilaire justifies his whole project as a return to the approach of the classics, particularly to Aristotle. The problem with this method—he argues—is that it was only an intuitive method. While intuition related distant parts such as pectoral fins and human hands, the "theory of analogues" allows us to relate parts that ancients were not able to see as connected, such as the shoulders of fishes and humans (Geoffroy Saint Hilaire 1818, p. xxxiv). The method of connections, as explicated by Geoffroy in his theory of analogues, was the method used by 19th-century morphologists to compare organismal structures: homologous parts, however they differ in form and size, are formed of the same elements, in the same number, and with the same connections. To use Owen's classic example, all vertebrate extremities belong to the same type (the vertebrate limb) because one can transform any limb (e.g., a horse's limb) into any other (e.g., a human's limb) by modifying the size and distances between the bones that constitute a limb.[8]

Thompson acknowledged that his method of transformations, just like Aristotle's method of the more and the less, is "a method of comparison of *related forms*" (Thompson 1917, p. 725; our emphasis).

> The chief difference between Aristotle's point of view and ours seemed merely to be that he limited his comparison, or his concept of homology, to the species of a single "genus" whereas the evolutionary morphologist seeks (not always with success), to trace detailed homologies between one Aristotelian genus and another. (Thompson 1929, p. 50)[9]

In order to relate forms at higher levels of organization, comparative morphology abstracts away shape to concentrate on the organizational relationships among the parts or subparts of an organism (Benson 1982). In this context, "form" does not just mean "shape," but also includes structure (Richter and Wirkner 2014, p. 340), therefore allowing morphologists to compare distantly related organismal structures, such as limbs and fins.

In some passages, Aristotle did note correspondences among wider animal groups by virtue of the locations and connections of those parts within the whole body. For instance, he relates the human mouth to birds' beaks (*PA* II.16, 659b20-26) and the whole-body plan of cephalopods and testacean mollusks.[10] Nonetheless, the method of the more and the less is certainly closer to Thompson's method of transformations than to the method of connections. In *G&F*, Thompson introduced the idea of comparing related biological forms ("the outline of an organism, ... or a part thereof: such as a fish, a crab, or a mammalian skull"; Thompson 1917, p.724) by inscribing their shape in a coordinate system and transforming this shape by means of the mathematical simulation of physical forces whose expression can be visualized in a deformation grid. In this way, the transformation of a figure generates other figures that correspond to real forms. As recognized by Thompson, Aristotle's method of division is the first attempt in the history of biology in comparing the *shape* of biological parts:

> Our enquiry lies, in short, just within the limits which Aristotle himself laid down when, in defining a "genus," he shewed that … the essential differences between one "species" and another are merely differences of proportion, of relative magnitude, or (as he phrased it) of "excess and defect" …. It is precisely this difference of relative magnitudes, this Aristotelian "excess and defect" in the case of form, which our coordinate method is especially adapted to analyse, and to reveal and demonstrate as the main cause of what (again in the Aristotelian sense) we term "specific" differences. (1917, p. 726)

In his later article on the more and the less, Thompson is even more explicit in how in translating the *History of*

[8] While the application of the method of connections led to the realization of its limits (for instance, certain elements might be fused or even be absent in certain groups as compared to others, such as digits in the horse limb), the topological method allowed transit across widely (apparently) unrelated animal forms.

[9] Aristotle does make "analogical" comparisons across kinds, such as between lung and gills, between feathers and scales, or between different kinds of wings (e.g., insect and bird wings). But these comparisons are based on function and not on shape or structure, what Owen called analogies as opposed to homologies.

[10] Aristotle writes that despite the apparently striking morphological differences in the location of their limbs (cephalopods have their feet towards the "front," while in testacean mollusks limbs project out from the side), when looking at the disposition of internal parts, "the configuration of the body" is alike. And by this likeness he means, in modern parlance, topological sameness, since a topological deformation (bending a straight line) is used to transform one digestive tract into the other (*PA* IV.684b20-25) (see Lennox 2002, pp. 311–312).

Animals, he interpreted Aristotle's use of the phrase "excess or defect" as the method of comparative morphology:

> The technical phrase "excess or defect" is sometimes used, especially by Aristotle, in a sense which is obviously not the arithmetical one, though it must be more or less analogous thereto. A single instance must suffice. In the first chapter of the *Historia Animalium*, Aristotle tells us that, within the limits of a "genus", such as Bird or Fish, the difference between one form or species and another is of the nature of 'excess or defect'; that their corresponding parts differ in property or accident, or in the degree to which they are subject to this or that property or accident, or in number, or in magnitude—in short always, after some fashion or other, in the way of excess or defect. When I translated the *Historia Animalium* many years ago, I took this statement to be neither more nor less than a foreshadowing of our own comparative morphology. I supposed that Aristotle would regard each species of bird much as a modern morphologist does; that he would recognise the correspondence or homology of their several parts; and that he saw, better perhaps than many morphologists do, how the differences between these corresponding parts are essentially quantitative differences, or 'differences of degree.' (1929, p. 55)

Thompson's interpretation passed unnoticed by Aristotle scholars for a long time. Only in a paper by Lennox (1980, fn 2; see also Lennox 1987) do we find an explicit reference to Thompson in discussing the meaning of the more and the less, which he interprets precisely as a challenge to the typological view of Aristotle. The mathematician René Thom later became aware of and was fascinated by Aristotle's use of the method of division in his biological works. According to Thom, the equivalence by excess or defect is akin to topological equivalence: each *genos* is subdivided into a subset of *eidê* whose representatives have an identical organization (the same "type") and, in turn, experience quantitative variations (Thom 1990). As Lennox has noticed, our modern expression for the phenomenon of differing by more and less is "continuous variations" or "variations on a common theme" (Lennox 1987), both key concepts in the morphological study of types.

As indicated above, in the morphological tradition two forms belong to the same type if one form can be transformed into the other. Therefore, the morphological investigation of types entails, by definition, the study of their transformations. In this sense, morphology does not deny variation, as some have claimed (Sober 1980). Rather, morphological types can be interpreted as abstract models that capture the extent and the limits of the variations a structure can experience (Young 1993). The same claim applies to Aristotle: while the "mythic Aristotelian biologist" depicted by the forgers of the essentialism story considers variations within types as accidental deviations from the essence of the species, the Aristotle emerging from the analysis of his actual biological practice and philosophy speaks of "a fascination with variation and how 'normal' and 'essential' he thinks understanding continuous variation is to understanding organisms" (Lennox 2017b). Thompson's interpretation of Aristotle's understanding of more and less variations on a general kind is in line with this interpretation.

Although visual representations of morphological spaces were introduced after Thompson's method of coordinate grid transformations (Bookstein 1977; Stone 1997) and the term "morphospace" was coined in the 1960s (Raup 1966), the idea of morphospace has been implicitly utilized throughout the history of morphology (McGhee 1999; Eble 2003). Indeed, it was Aristotle who first used anatomical diagrams, and some of them must have been highly schematic in representing kinds of parts (e.g., the womb of a viviparous quadruped) or kinds of relations among parts (e.g., of blood vessels to the uterus in viviparous animals, *GA* II.7, 746a8-22; cf. Lennox 2018). Furthermore, it has been argued that Aristotle's choice of parts as an object of inquiry inaugurates theoretical biology, since it makes it possible to overcome the task of verifying diversity to discover the logic of form, namely the limited number of combinations of parts and their variations (Crubellier and Pellegrin 2002). This was clearly not the goal of Aristotle, for whom the method of division was a means to understanding the causal essence of actual animal kinds, but it certainly made it possible. In separating the shape and structure of parts from their material constitution and their functional roles, the method of division became, in Thompson's hands, independent of Aristotle's purposes. As acknowledged in *G&F*, the comparison of actual forms is, in this regard, a subdiscipline of a wider science of form: "Our own study of organic form, which we call by Goethe's name of Morphology, is but a portion of that wider Science of Form which deals with the forms assumed by matter under all aspects and conditions, and, in a still wider sense, with forms which are theoretically imaginable" (1917, p. 1026).

While the Aristotelian method of division applies to parts and cannot deliver animal kinds, the results of the division of parts are also applied to the identification of animal groups through the recognition of correlations among these parts (Lennox 2005).[11] For instance, the acknowledgment that certain animals consistently display the same

[11] There is a debate among Aristotle scholars regarding whether the conceptual schema *genos/eidos* is applicable to animal groups, such as birds or eagles (Balme 1987b), or parts, such as beaks or wings (Pellegrin 1987).

parts (wings, feathers, beaks, two legs) makes it possible to distinguish "birds" as an animal kind. Once these general kinds are distinguished by means of the identification of the general characters they share, these traits can be subdivided into more and more specific traits (e.g., beaks and legs with different shapes and lengths) (Lennox 2017b). This leads to an approach to the definition of animals that radically differs from the concept of logical universal (Furth 1987). Animal kinds are distinguished from one another not by one trait that is necessary and sufficient for membership in a kind, but by a complex set of attributes that cannot be presented in a single line of differentiation. What is important for Aristotle is not that particular kinds of organisms have a particular attribute, but how those attributes are correlated with other kinds of attributes in other kinds of organisms. And ultimately to understand why, for instance, all animals that breathe have lungs, why all animals with lungs have windpipes, why if they have windpipes they must have esophaguses, and if so why they must have some method for closing the windpipe while eating, and so on. Grasping such commensurately universal relations is the first step to grasping causes (Lennox 2017a). Again, Aristotle appears here as the founder of a major research program in the morphological tradition, namely the study of *morphological correlations*,[12] a concern absent from taxonomy, where species are described "part by part" (Gould 1971, p. 233). D'Arcy Thompson vindicates this integrative approach to living form in Aristotle and criticizes morphologists who, in focusing on the study of homology, often forget the integrated nature of organismal variation:

> The biologist, as well as the philosopher, learns to recognise that the whole is not merely the sum of its parts. It is this, and much more than this. For it is not a bundle of parts but an organisation of parts, of parts in their mutual arrangement, fitting one with another, in what Aristotle calls "a single and indivisible principle of unity"; and this is no merely metaphysical conception, but is in biology the fundamental truth which lies at the basis of Geoffroy's (or Goethe's) law of "compensation," or "balancement of growth." (1917, p. 704).

> … the morphologist, when comparing one organism with another, describes the differences between them point by point, and "character" by "character." If he is from time to time constrained to admit the existence of "correlation" between characters (as a hundred years ago Cuvier first showed the way), yet all the while he recognises this fact of correlation somewhat vaguely, as a phenomenon due to causes which, except in rare instances, he can hardly hope to trace; and he falls readily into the habit of thinking and talking of evolution as though it had proceeded on the lines of his own descriptions, point by point, and character by character. (1917, p. 727)

To sum up: Aristotle's study of animal form shares with Thompson's crucial aspects that allow us to situate them both in the morphological tradition. First, the Aristotelian method of division is better comprehended as the first formulation of the method of transformations, instead of as an embryonic taxonomic method. When applying this method to compare body parts, Aristotle distinguishes form from function. This separation enables him to carve living nature at its joints and lays the groundwork for the study of homology. Second, Aristotle's study of correlations endorses an integrative approach to organismal form that differs from taxonomical groupings of living entities as sets of independent traits. Finally, the method of transformations and the combination of parts opens the way for the theoretical exploration of possible forms.

However, two caveats need to be addressed. Firstly, our differentiation between taxonomy and morphology does not imply they are entirely separate fields. On the contrary, classification can rely on, and according to some, needs to rely on morphological data that capture homology relationships (Patterson 1982). Secondly, our presentation of the Aristotelian method as a morphological method does not entail that Aristotle's and Thompson's theories of form were projects in pure morphology, independent of their explanatory agendas. Instead, in the following section we show how both Aristotle's and Thompson's study of the relatedness of forms prepare the ground for a causal explanation of parts and their correlations. While they emphasized different kinds of causes, we argue that they were both attempting to understand the same kind of explananda. This kind of causal explanation of form differs from that inaugurated by Darwin's theory of natural selection, which was conceived as a solution to the problem of species, and not to the problem of form.

[12] While Aristotle's understanding of correlations is indissociable from his causal interpretation of these correlations, the identification of correlations between parts has proved to be one of the greatest tools of morphology to unravel functional and developmental correlations (Olson and Miller 1958). As Thompson puts it: "if … diverse and dissimilar fishes can be referred as a whole to identical functions of very different coordinate systems, this fact will of itself constitute a proof that variation has proceeded on definite and orderly lines, that a comprehensive 'law of growth' has pervaded the whole structure in its integrity, and that some more or less simple and recognisable system of forces has been at work" (Thompson 1917, p. 728).

The Explanation of Form

In E. S. Russell's words, for Darwin "the chief problem was not the evolution and differentiation of types of structure, but the mode of origin of species" (1916, p. 232). The problem Darwin sought to solve was the *species problem* encountered by taxonomists, given the practical difficulties to distinguish varieties and species (Gayon 1998). It was the acknowledgment of the imprecision of specific borders, based on the new evidence from biogeography and paleontology, that led Darwin to argue that the differences between varieties and species were ones of degree, not of kind (Lennox 2017b). In turn, it was this taxonomical fuzziness between varieties and species that allowed him to conceive the possibility of their historical transformation, as opposed to the belief in the independent, discrete origination of each species (Hull 1965). In other words: the gradual transitions that from a synchronic point of view reflected the difficulties of classification, were seen as the expression of diachronic transitions (Sloan 2009).

As pointed out above, neo-Darwinians and their philosophical defenders have presented this theoretical shift as a revolution against Aristotelian essentialism (Ruse 1979). However, given that Aristotle's essentialism has nothing to do with the sort of typological essentialism characterized by neo-Darwinians, it might be argued that Darwin did not really have to deal with it. Moreover, far from being radical antagonists, Aristotle and Darwin might be even regarded as "kindred spirits," linked by a shared belief in the continuous variation of form (Lennox 2017b). The issue at stake here is the meaning of form. In Aristotle, the term *eidos* is employed to denote both the formal aspect of an animal, as distinct from its matter, and the distinctive forms that kinds such as "bird" can encompass. For instance, eagles or storks are distinct forms of the kind bird. "Form" can serve as an appropriate translation in both cases (Lennox 2017b). However, in Darwin's times, the problem of form and the problem of species were distinct problems, addressed by distinct disciplines, namely morphology and taxonomy, and with different methodologies. The *Origin of Species* simultaneously solved these two problems by providing two kinds of explanation: the theory of natural selection addressed the problem of the origination of species, as defined in the field of taxonomy, while the theory of descent with modification provided a historical explanation of the problem of form, as delineated by comparative morphology.

With the consideration of natural classes as populations composed of variable individuals connected by reproduction, the ontological core of Darwinism is no longer form but species, and evolution is no longer seen as a metamorphosis, but as the result of intrapopulational variation (Gayon 1998). In this view, the species concept is defined by the speciation that results from the selective process, by means of which the origin of classes (i.e., speciation) is explained (Gayon 1998). Natural selection was progressively conceptualized as the mechanism by means of which the spreading and removal of variations take place. The reformulation of selection by population genetics, where organisms are disintegrated into collections of independent traits with associated fitness values, strengthened the atomistic trends that, according to some, were already perceptible in Darwin's philosophy (Gayon 1998). Therefore, the exclusion of morphology from the Modern Synthesis comes precisely from replacing the problem of form with the problem of species.

While the theory of natural selection solved the species problem, the theory of descent with modification was Darwin's solution to the problem of form. In the *Origin*, Darwin used the facts of morphology to demonstrate the fact of evolution (Darwin 1859, Chaps. 6 and 13). According to the new phylogenetic concept of homology, two forms are related because they come from (i.e., they were transformed from) a common ancestor, but types, including homologies and body plans, continued to be defined on the basis of the topological criteria used by pre-evolutionary morphology (Brigandt 2003). Evolutionism did change the epistemic goals of comparative anatomists and embryologists, who no longer aimed to reveal structural affinities, but to reconstruct the tree of life. Nonetheless, structural identities continued to be established on the basis of anatomical and embryological criteria, and not the other way around (Amundson 2005).[13] Certainly, the phylogenetic purpose was entirely foreign to Aristotle, but this was also the case for D'Arcy Thompson. As will be argued in the remainder of this section, both Aristotle's and Thompson's projects were endeavors in causal morphology, albeit with a focus on different types of causes.

The overall goal of Aristotle's biology was not the goal of theoretical morphology, to put it in modern parlance. Aristotle's approach is a teleological approach, where final causality, or explanation by reference to developmental goals and organic functions, is the primary explanation. The central explanatory task of his zoological treatises, as

[13] This does not mean that the comparative study of form cannot be used for phylogenetic purposes. On the contrary, the reconstruction of phylogenetic relationships makes extensive use of morphological data. But the labor of comparative biology is epistemologically prior to the establishment of genealogical relationships, given that they are inferred from the acknowledgment of similarity among parts, and not the other way around (Patterson 1982; Rieppel and Kearney 2002). In the context of evo-devo, it has also been argued that the developmental explanation of homology depends on the previous identification of structural units, based on morphological criteria (Roth 1991; Wagner 1996). In this sense, evolutionary morphologists today seek to identify homologs by means of "operational definitions," i.e., definitions that are necessary to reach a causal explanation without being themselves explanatory (Bolker 2000).

undertaken in the *Parts of Animals* and the *Generation of Animals*, is to show that animals have the parts they do, arranged, structured, and related as they are, because of the peculiar activities that constitute their ways of life. Thus, if birds differ "from [one] another in the excess and deficiency of their parts, that is according to the more and less," it is because of their different ways of life; e.g., shorebirds have long legs and long necks because of their distinctive way of life (*PA* IV.12). For Aristotle, the way of life of animals takes precedence (conceptual priority) over their particular activities, character traits, and parts (Lennox 2009, 2017a). In this regard, his study of organismal form is much closer to functional and ecological morphology than to theoretical morphology.[14]

As detailed in the previous section, the general features that characterize the parts and body plans of animal kinds, such as birds or fishes (the morphological "types"), always come in varied, particular forms associated with particular ways of being. But the method Aristotle developed to divide such kinds into specific forms makes it possible to understand the "unity in diversity" in a way that was fully alien to the taxonomical focus on distinguishing species from varieties. Furthermore, the structural characterization of form and the establishment of morphological correspondences has a methodological (not conceptual) priority over developmental and functional explanations of form. As indicated above, the comparative study of form sets the stage for providing causal explanations as to why different animals possess the distinct parts that they do. Once these causal explanations are found, the description and the explanation of the essence of an animal kind are indeed coincident: "it is an animal's peculiar way of life and the activities that are required by that way of life that explain why each animal has the parts it has with those more and less variations characterized in *HA*" (Lennox 2017b). Aristotle's biological essentialism has, therefore, "nothing to do with the 'mythic' version" promulgated by the essentialist story (Lennox 2017b).

Thompson concurred with Aristotle on the need to identify more than one cause to explain form and was fully aware of the incompleteness of his theory of form (Gould 1971). But instead of focusing on final causes, he prioritized efficient causes, understanding biological patterns as an expression of forces and physical processes. In this regard, Thompson stands as a pioneer in advocating biophysics—rather than biomathematics—as a central discipline in biology. In particular, the diagrams of transformation are not "a mere framework for description," but they might be the result of efficient causes (Kemp 2011, p. 8). As Thompson explains:

> The study of form may be descriptive merely, or it may become analytical. We begin by describing the shape of an object in the simple words of common speech: we end by defining it in the precise language of mathematics; and the one method tends to follow the other in strict scientific order and historical continuity …. Next, we soon reach through mathematical analysis to mathematical synthesis; we discover homologies or identities which were not obvious before, and which our descriptions obscured rather than revealed …. Lastly, and this is the greatest gain of all, we pass quickly and easily from the mathematical conception of form in its statical aspect to form in its dynamical relations: we pass from the conception of form to an understanding of the forces which gave rise to it; and in the representation of form and in the comparison of kindred forms, we see in the one case a diagram of forces in equilibrium, and in the other case we discern the magnitude and the direction of the forces which have sufficed to convert the one form into the other. (Thompson 1917, pp. 719–720)

As noted by Arthur (2023), Thompson's morphological transformations can never occur in evolution, as the evolution of form involves developmental repatterning rather than the direct conversion of one species' adult form into another's. Thompson, like any other student of form relationships, was fully aware of this fact. However, the conventional interpretation of morphological transformations is that the simplicity of some of these transformations often plays a heuristic role in uncovering causal explanations, whether related to phylogenetic relationships or to developmental mechanisms like allometric growth.

Regarding the explanation of morphological transformations, Thompson was not a reductionist but a pluralist on causation, and it is in this context that he uses efficient explanations of form, countering both teleological and historical explanations, as a demonstration of the sufficiency of physical principles such as growth laws (Dresow 2020). Moreover, the kind of teleology he opposed, namely that of neo-Darwinian panadaptationists, had little to do with Aristotle's teleology (Gotthelf 1987). Aristotle sometimes explicitly rules out final causes for explaining certain traits and attributes their nature to material-efficient causes.[15]

[14] This functional approach to living beings by no means entails that Aristotle was a Panglossian, a priori teleologist. On the contrary, he explicitly objects to the idea that every difference among animal forms should be explained in teleological terms. Instead, he argues that some biological traits necessarily derive from the formal and functional properties of other parts (*PA* IV.677a16-19). See footnote 15 for an example.

[15] For instance, in discussing a species of octopus with only one, instead of two, rows of suckers on its "arms" he explicitly explains it as a consequence of structure—this is a small octopus with very slender arms, so there is only room for one row of suckers. He then says: "It is

More importantly, Aristotle's teleological explanations are always rooted in a deep understanding of the qualities of organismal matter, as well as the topological and functional constraints on what is best for each particular being. More and less variations of structures generate a space of forms that widely exceed extant ones, but functional and material constraints restrict this space to the space of the actual. As Aristotle noted (*PA* III.1, 662 a33-b16; *PA* IV.12, 693a10-24), it is because birds eat certain kinds of food that their beaks have the shapes they have, yet the sizes and forms of beaks are constrained due to their composition from limited matter with distinct properties. This theme is continued in *GA*, where the assertion is that parts result from successive differentiations rather than mere aggregations. Consequently, the shaping of beaks is a consequence of actual ontogenetic transformation. This is precisely what Thompson argues for in Chap. 16 of *G&F*:

> When, after attempting to comprehend the exquisite adaptation of the swallow or the albatross to the navigation of the air, we try to pass beyond the empirical study and contemplation of such perfection of mechanical fitness, and to ask how such fitness came to be, then indeed we may be excused if we stand wrapt in wonderment, and if our minds be occupied and even satisfied with the conception of a final cause. And yet all the while, with no loss of wonderment nor lack of reverence, do we find ourselves constrained to believe that somehow or other, in dynamical principles and natural law, there lie hidden the steps and stages of physical causation by which the material structure was so shapen to its ends. (1917, p. 673)

Later in his life, well after the publication of *G&F*, Thompson favored a Platonic interpretation of the Aristotelian notion of type. In his 1929 article on the different meanings of "excess and defect" in Greek mathematics, Thompson argues that the technical meaning of this phrase in the *History of Animals* demands a Platonic interpretation:

> For I take it now that Aristotle was thinking, *more Platonico*, of all the fowls of the air as mere visible forms or *εἴδη*, mere imperfect representations of or approximations to, their prototype the ideal Bird. Just as we study the rational forms of an irrational number, and through their narrowing vista draw nearer and nearer to the ideal thing, but always fail to reach it by the little more or the little less: so we may, as it were, survey the whole motley troop of feathered things, only to find each one of them falling short of perfection, deficient here, redundant there: all with their inevitable earthly faults and flaws. Then beyond them all we begin to see dimly a bird such as never was on Sea or land, without blemish, whether of excess or defect: it is the ideal Bird, the παράδειγμα ὅ ἐν Οὐρανῳ ανάκειται.[16] (1929, p. 50)

However, this interpretation does not account for the connection between the description and the explanation of form we have argued for in this section, and that is the basis for the current revisiting of Aristotle's biological treatises after the resurgence of the problem of form brought about by evolutionary developmental biology. While the problem of species was instrumental to the Darwinian variational approach to evolution, the problem of form is regarded as the core research agenda of evo-devo (Love and Raff 2003): it is only by reinstating the importance of form, as revealed by homologies and novelties, that development can be reintegrated into evolutionary theory. If the neo-Darwinian approach to evolution treated development as irrelevant, it was precisely because it previously neglected the problem of form by reducing evolution to changes in gene frequencies due to selection acting on independent traits. Evo-devo attempts to recover the research program of evolutionary morphology from a mechanistic, developmental perspective (Love 2006). The problem of form emerges again as the main explanandum of evolutionary biology, but instead of using morphological relationships as evidence to reconstruct phylogenetic relationships, evo-devo aims to understand the developmental causes of morphological evolution. In this new theoretical context, it is not surprising that both Aristotle's and Thompson's theories of form are being reevaluated. Philosophers have argued that evo-devo entails a neo-Aristotelian essentialism where organismal essences are no longer identified with a set of fixed morphological structures, but with a dynamic, developmental bauplan that explains the extent and limits of the variations on general architectural themes (Walsh 2006, 2015; Nuño de la Rosa 2010; Lennox 2017a; Austin 2018). This philosophical view aligns with the mechanistic reinterpretation of typology endorsed by practitioners of evo-devo, where homologies and body plans are no longer seen as idealized morphological abstractions, but instead, as structural organizations maintained through shared generative processes (Shubin and Alberch 1986; Wagner 1989, 2014; Rieppel 2007). The understanding of the flexible and dynamical nature of

not, then, because it is best that they have this feature, but because it is necessary owing to the distinctive account of their substantial being" (*PA* IV.9 685b12ff). That is, not only does he invoke a structural feature as necessitating the attribute in question, he is claiming that that structural feature is a defining feature of the nature of this kind of octopus, and he is explicitly ruling out a teleological explanation.

[16] "[P]aradigm set up in Heaven": Thompson is quoting Plato's *Republic* IX.592b2.

Aristotle's essentialism has required reading Aristotle in the light of new translations and interpretations of his biological treatises.[17] Thompson's work as a translator and interpreter of Aristotle, as well as his formulation of the method of the more and the less as a method of geometric transformations, have been instrumental in this regard.

Analyzing how form, function, and development are intertwined in Aristotle's biology, and how his causal understanding of form influenced Thompson and echoes the research programs of functional morphology and evo-devo is outside the scope of this article. Rather, our claim is that the explanation of form depends on how phenotypic diversity is previously organized. The different interpretations of Aristotle might explain why he was condemned by the Modern Synthesis, but fascinated pre-Darwinian 19th-century comparative biologists, as well as early 20th-century organismal biologists such as Russell (1930) and Thompson himself, and has recently aroused a renewed interest from evo-devo researchers. Hence, looking at Aristotle as a taxonomist or as a morphologist determines the way we look at the relevance of his biological work in our current evolutionary framework. Misinterpretations of intellectual ancestors are perpetuated through the reading of biased secondary literature and have consequences on contemporary scientific debates. Historical reconstructions of the scientific past often serve propagandistic purposes of present science and the use of Aristotle's biology to emphasize the radicality of the Darwinian revolution illustrates the perils of a Whig history of science. This does not mean that the past has nothing to tell us about present science. As we outlined at the beginning of this essay, phylogenetic approaches to current scientific problems can be most helpful. D'Arcy Thompson's interpretation of Aristotle's expressions "excess and defect" and "the more and the less" as revealing a morphological method of transformations restored a view that was already implicit among pre-evolutionary comparative anatomists and that had faded with the fall of evolutionary morphology and the rise of neo-Darwinism. With the resurgence of the problem of form in ongoing debates in evolutionary biology, Thompson's views of Aristotle regain significance, and this intermittent, intellectual tradition is once again alive among practitioners of evo-devo.

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[17] Both Walsh (2015) and Austin (2018) refer to the contemporary reading of *genos* and *eidos* among Aristotle's scholars.

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