> The forms of the spicules are the result of adaptation to the requirements of the sponge as a whole, produced by the action of natural selection upon variation in every direction.
>
> *Edward A.Minchin (1898, 569)*

> It would scarcely be possible to illustrate more briefly and more cogently than by these few words [. . .] the fundamental difference between the Darwinian conception of the causation and determination of Form, and that which is based on, and characteristic of, the physical sciences.
>
> *D'Arcy Thompson (1992 [1942], 693), commenting on Minchin*

1 Structure and Function

1.1 The Cuvier-Geoffroy Dispute

In October 1829, Pierre-Stanislas Meyranx and Laurencet (the latter so obscure his full name remains unknown) submitted, to the Académie des Sciences in Paris, a memoir purporting to demonstrate a deep unity of form linking vertebrates and mollusks (following Appel 1987, chap. 6). Take a vertebrate. Bend it backward so that the nape touches the anus – the arrangement of its internal organs now matches, they argued, that of a cephalopod. After a long wait, Pierre André Latreille and Étienne Geoffroy Saint-Hilaire were assigned to prepare a report on the memoir. Delivered on February 15, 1830, their report brought to a boil long-simmering tensions between Geoffroy and his erstwhile friend Georges Cuvier.

One of their deepest disagreements concerned whether anatomy should be organized around Unity of Type (Geoffroy) or Conditions of Existence (Cuvier) – "whether animal structure ought to be explained primarily by reference to function or by morphological laws" (Appel 1987, 2). In 1812, Cuvier separated the animal kingdom into four *embranchements*, each characterized by a unique arrangement of functionally integrated parts. Individual species realized this arrangement in a manner befitting their particular form of life. Structural correspondences could be traced within *embranchements*, but not between them.

Geoffroy's "philosophical anatomy," by contrast, sought correspondences spanning the entire animal kingdom. Notoriously, he claimed that vertebrates are arthropods turned upside-down – a hypothesis whose apparent absurdity has not stopped it from receiving "a measure of molecular support" (de Robertis 2008). Meyranx and Laurencet's memoir enabled Geoffroy to connect vertebrates to mollusks as well. These correspondences pointed toward general morphological laws inexplicable by species' particular conditions of existence.

The official debate before the Académie ended in April 1830, but the disagreement persisted until Cuvier's death in May 1832. Though Cuvier was

widely recognized as the "winner" of the debate, Geoffroy's views remained influential – his "loss" hardly dampened the prospects of philosophical anatomy. Indeed, conflicts between structuralist and functionalist visions of biology, between Unity of Type and Conditions of Existence, are persistent presences haunting the history of biology, from its origins in ancient Greece right down to contemporary debates within evolutionary theory. This Element aims to make sense of them.

1.2 Structuralism and Functionalism I

Historians, philosophers, and biologists alike have analyzed the history of biology (in whole or part) in terms of conflicts between structuralists and functionalists (Coleman 1977 [1971]; Russell 1982 [1912]; Asma 1996; Amundson 2005). Shortly after the Cuvier-Geoffroy debate, similar tensions arose between Richard Owen (e.g., 2007 [1849]) and Charles Darwin (e.g., 1964 [1859]). In the twentieth century, the functionalist modern synthesis (Dobzhansky 1982 [1937]; Mayr 1982 [1942]; Simpson 1984 [1944]) was challenged by the structuralist alternatives of Richard Goldschmidt (1982 [1940]) and Otto Schindewolf (1993 [1950]). The rise of evolutionary-developmental biology (evo-devo) generated and continues to generate structure/function disputes (Hughes and Lambert 1984; Alberch 1989; Amundson 2005; Wagner 2014). Related conflicts arise from biophysical approaches to organic form (Webster and Goodwin 1982, 1996; Ho and Saunders 1993; Kauffman 1993; Newman and Bhat 2008), which recapitulate themes from the Thompson/Minchin conflict quoted in the epigraph. Going backward in time, Empedocles' explanation of plant growth in terms of their earthen roots and fiery trunks offered an early structuralist view, against which Aristotle raised a functionalist critique (Irwin and Fine 1996, 87–88). The list could be extended *ad nauseam*.

My decision to rattle off examples before saying what structuralism and functionalism *are* is, perhaps, frustrating. But to say what they are is difficult, for they have survived thousands of years of drastic theoretical change. If structuralism is a meaningful category, it must capture how Empedocles, Richard Owen, D'Arcy Wentworth Thompson, and Pere Alberch (*inter alia*) are similar; if functionalism is a meaningful category, it must capture how Aristotle, Georges Cuvier, Ernst Mayr, and Eva Jablonka (*inter alia*) are similar. And these similarities must not be so vague as to render the designations vacuous.

This Element develops a novel account of structuralism and functionalism. The main difficulty, as I see it, stems from analyzing structuralism and functionalism as *positions* of some strange kind: contentful, yet able to survive even

radical theoretical change. I focus instead on structuralist and functionalist *explanatory strategies* – abstract schemas that, uncommitted to any particular theory, capture underlying patterns in the explanation of organismic form.

Like most work on this topic, my analysis focuses on explanations of morphological form in multicellular organisms. However, structure/function disputes themselves are not so limited. They arise, for instance, in the study of genome evolution, for the genome "has an evolutionary life of its own" (West-Eberhard 2003, 19), as well as in microbial evolution (e.g., Sapp 2009, 294–99). They may even arise in the study of biological function itself, in conflicts between organizational (Mossio, Saborido, and Moreno 2009) and selected effect (Garson 2017) accounts thereof. Space constraints have narrowed my vision, but I hope my analysis will prove valuable beyond the study of multicellular form.

1.3 Three Approaches: Stances, Paradigms, Strategies

Philosophical analysis of structuralism and functionalism has two core aims: to *explain* features of the history of biology and to *provide guidance* to those who find themselves in present-day structure/function disputes. These can be further specified in terms of five desiderata. An analysis of structuralism and functionalism should

1. capture what all structuralists have in common, in virtue of which they are structuralists, and likewise for functionalists.
2. be sufficiently contentful to explain why structuralist and functionalist biologists behave as they do.
3. explain why structuralism and functionalism have persisted across radical theory change in biology.
4. clarify how, why, where, and what kind of empirical evidence is relevant to structure/function disputes.
5. explain, not just why structuralism and functionalism conflict, but also how they can be and have been integrated.

The first two desiderata capture basic constraints on explanatory adequacy. The first is intuitive: for any account to qualify as an account of structuralism and functionalism at all, it must tell us what structuralism and functionalism *are*. The second is comparably intuitive: for the account to be enlightening, the characterizations offered should allow us, not merely to *identify* structuralists and functionalists, but to explain why they engage in biological inquiry as they do.

The latter three desiderata identify particular explanatory targets. The third concerns the fact that structuralism and functionalism *have* persisted across

radical theory change. We need an explanation of how this is possible and why it has happened. The fourth concerns the fact that biologists engaging in structure/function disputes bring empirical evidence to bear on them. Even if structure/function disputes have a nonempirical core, we still need to understand how and why empirical evidence becomes relevant.

The fifth concerns the fact that interactions between structuralism and functionalism are not exclusively antagonistic. Their integration has occupied less philosophical attention than their conflict; accordingly, I devote significant space to documenting that it occurs (Section 3). Even without such documentation, however, the long-term persistence of structuralism and functionalism should lead us to expect that both capture important aspects of the biological world and thus that it should be possible to integrate them.

Satisfying all five desiderata simultaneously is challenging. The first two pull in opposite directions. To satisfy the first, an account must be sufficiently abstract to capture thinkers separated by deep theoretical gulfs – but this abstraction must not cost the account its explanatory power. The third and fourth likewise exert opposed forces. To satisfy the third, an account must explain why empirical evidence has not put an end to structure/function disputes – but this explanation must not render empirical evidence entirely irrelevant. We may hope to find an acceptable compromise between both sets of opposing pulls, but it is a difficult tightrope to walk.

Until all five are satisfied, our understanding of structuralism and functionalism is lacking. *How* they are to be satisfied – whether by a single account or in a more piecemeal fashion – remains an open question. I will argue that, by treating structuralism and functionalism not as *positions* (or similar) held by particular inquirers, but rather as *explanatory strategies*, we can satisfy all five. Moreover, my account augments the explanatory power of two recent analyses (Boucher 2015; Winther 2015) that both capture important aspects of the issue, but that are not sufficient either individually or jointly.

Boucher (2015) analyzes structuralism and functionalism as stances (Van Fraassen 2002; Boucher 2014). Stances are clusters of attitudes, not sets of beliefs – they are not propositional and not truth apt. The adoption of stances is driven by one's values (both epistemic and not) and is justified pragmatically. On this view, structuralists and functionalists are distinguished by how they *approach* the organic world, which shapes but does not determine what they *believe* about it. Their disagreement concerns which features of the organic world are most important to capture in biological theorizing. Functionalists take explaining organism-environment fit as a central explanatory task, while structuralists are more concerned with deep similarities between species living in rather different environments.

Boucher's analysis satisfies the first and third desiderata. It identifies a specific feature – adoption of a particular stance – by which structuralists and functionalists can be identified and distinguished. Moreover, because adopting a stance does not require endorsing any particular belief, stances can survive even radical theoretical change. Thus Boucher can explain empirical advances have failed end the debate. Though not uninfluenced by empirical evidence, stances are not (dis)confirmed by it.

The second, fourth, and fifth desiderata are trickier. Stances capture what all functionalists (structuralists) have in common, but highly abstractly, which limits what Boucher can explain. Knowing merely that a biologist adopts a particular stance, one cannot predict much about their research practices. Precisely because stances have a loose, nonlogical relationship with theories and evidence, Boucher's account says little about what types of evidence functionalists (structuralists) will gather, what kinds of theories they will develop on that basis, what kinds of explanations they will favor, and how they will conduct empirical disputes. Moreover, because structuralist and functionalist stances involve incompatible values (one cannot simultaneously foreground and background adaptation), stances cannot be integrated. Accordingly, Boucher (2019) limits nonantagonistic interactions between structuralism and functionalism to pluralistic tolerance.

Winther (2015) analyzes structuralism and functionalism (or "adaptationism") as Kuhnian paradigms. Paradigms include diverse elements (see Winther 2015, 472 for a full list); most important here is that they include *both* theoretical and empirical *and* nonpropositional commitments, including explanatory standards, research questions, and methods. Proponents of the functionalist paradigm treat organism–environment fit as the central evolutionary problem and natural selection as the most important explanatory resource for solving it; they may also endorse methodological adaptationism (Godfrey-Smith 2001). Proponents of the structuralist paradigm are most concerned with problems of how structures form and emphasize the role of "mathematical laws of development and physiochemical morphogenetic mechanisms" in explaining this (Winther 2015, 473).

Compared to Boucher's, Winther's analysis has inverse virtues and vices. Because paradigms involve structured relationships between value judgments (including those characteristic of Boucher's stances), methods, and particular beliefs, Winther's analysis does an excellent job explaining why particular biologists conduct inquiry as they do, including why they seek out particular kinds of evidence. Moreover, while distinct paradigms may involve incompatible values, their other elements can be complementary, so Winther (2015, sec. 21.3.3) has the resources to explain not just "imperialist" but also "collaborative" interactions.

Winther's analysis purchases these virtues at the cost of generality. Whereas stances are persistent by design, paradigms are ephemeral by design. They characterize complex commitments of particular scientific communities over comparatively short temporal durations. The structuralist and functionalist paradigms Winther identifies are specific to contemporary evolutionary theorizing. Nor does Winther's account answer what it is that makes these paradigms structuralist and functionalist, respectively – what they have in common with past structuralist and functionalist paradigms. This is not a problem for Winther: his concern is to understand evo-devo, and paradigms are an appropriate tool. However, paradigms cannot furnish a *general* account of structuralism and functionalism.

Can we satisfy all five desiderata by conjoining the two accounts? The idea here is that scientists who adopt structuralist (functionalist) stances develop particular structuralist (functionalist) paradigms. What structuralist (functionalist) paradigms have in common is precisely that they include, among their many commitments, the adoption of a particular stance. Though the paradigms are short-lived, the associated stances survive their dissolution.

For the *explanatory* task, I think this combined approach is a good start, but incomplete: resources are needed beyond those Boucher and Winther provide (for the *normative* task, I have reservations about stances; Section 5.1). Structuralist (functionalist) paradigms share similarities beyond being motivated by shared stances, and these similarities are essential for explaining why the history of biology looks as it does. What is missing from is something that can both survive radical theory change (as paradigms cannot) as well as elucidate the empirical activities of structuralist (functionalist) biologists (as stances cannot).

Explanatory strategies provide this missing element. By "explanatory strategy" I mean a schema for constructing explanations that partially specifies:

- what constitutes an appropriate target *explanandum*
- what constitutes an appropriate *explanans*

By "partially" in "partially specifies," I mean that the schema must leave out certain key details, such that diverse theories can fill in these details in their own way. By "specifies," I mean that the schema must nonetheless clearly limit what counts as a legitimate way of filling in these details. By filling in details in accordance with this partial specification, the schema is converted into an explanation proper.

Explanatory strategies are independent of stances: one can offer a structuralist (functionalist) explanation without taking a stand on the significance of the *explanandum*. However, insofar as the phenomena foregrounded by structuralists

(functionalists) are especially amenable to structuralist (functionalist) explanation, explanatory strategies can help the stance account explain biologists' research practices. Explanatory strategies also allow us to recognize sequences of structuralist (functionalist) paradigms that all favor explanations that realize the same strategy. Explanatory strategies are a reusable resource for constructing paradigms and can outlive them. Finally, explanatory strategies can be integrated by constructing complex explanatory chains incorporating both of them.

It is thus *prima facie* plausible that an analysis of structuralism and functionalism in terms of explanatory strategies will satisfy all five desiderata, while also complementing both stance and paradigm analyses. But it is well known where the devil lurks.

2 Explanatory Strategies

2.1 Structuralism and Functionalism II

In this section, I make the case for analyzing structuralism and functionalism in terms of explanatory strategies. I begin by discussing a range of historical material that any such account must capture, using it to introduce important conceptual clarifications (Sections 2.1–2.4), then make my core case for the importance of explanatory strategies (Sections 2.5–2.6).

The first clarification concerns a common, but misleading, way of presenting the difference between structuralism and functionalism. It is sometimes stated that structuralists and functionalists disagree over whether form is explanatorily prior to function (structuralism) or vice versa (functionalism). For instance, E. S. Russell (1982 [1912], xi) asks, "Is function the mechanical result of form, or is form merely the manifestation of function or activity?" and Stephen Asma (1996, 12) writes, "the question was whether specific organic structure was the result of specific function or vice versa." However, while functionalists do, in an important sense, treat function as prior to form, structuralists do *not* treat form as prior to function *in the corresponding sense*.

The relevant sense of priority here is explanatory priority. In any given explanation, the *explanans* is explanatorily prior to the *explanandum*. To say that functionalists treat function as prior to form is thus to say that functionalists explain form (*explanandum*) by invoking the function served by that form (*explanans*) – and vice versa for structuralists. Note that this relativizes priority to particular explanations: what is *explanans* in one context may be *explanandum* in another.

This adequately captures the functionalist side of the dispute, but it mischaracterizes the structuralist position. This is best appreciated in the light of examples. For functionalists, consider Lamarck and Cuvier. Actually, it is tendentious to call

Lamarck (2011 [1809]) a "functionalist," as his theory is really a hybrid theory involving the interaction of two processes: (a) an orthogenetic tendency for lineages to increase in complexity over time (structuralist) and (b) a mechanism by which novel structures arise in response to new organismal needs (functionalist). For now, consider the latter only. As organisms change their behavior to meet new needs, their physiology changes, leading to structural modifications that are inherited by their descendants. In this way, novel structures arise to fulfill particular functions. For the functionalist portion of Lamarck's theory, structure is *explanandum*, function is *explanans*.

So also for Cuvier (Rudwick 1997), who explained the features of organisms in terms of their conditions of existence (Coleman 1964; Outram 1986; Appel 1987). Cuvier saw organisms as tightly integrated arrangements of anatomical parts, each particular arrangement being determined by the needs associated with an organism's particular form of life (Novick 2019). Once again, structure is *explanandum*, function is *explanans*.

So far, so good. But now consider how Richard Owen, arch-structuralist, attempted to refute these functionalist views. Not only did Owen not argue that structure explains function, his arguments altogether precluded that possibility. Consider Owen's (2007 [1849]) analysis of the bat's wing, the dugong's front fin, and the mole's forelimb (Figure 1). Each is adapted to a different function: the bat's wing for flight, the dugong's fin for swimming, and the mole's forelimb for digging. Nonetheless, each is structurally very similar, consisting of the same bones in the same arrangement. The same basic structure thus serves many functions.

Because of this one-to-many relationship between structure and function, Owen argued that function could not explain structural correspondences. Considering the bat's wing in isolation, one might try to explain how its underlying structure is suited to flying, but that structure's recurrence in the dugong's fin (swimming) and the mole's forelimb (digging) undermines that functional explanation. Moreover, that structure is not necessary for any of those functions, which are achieved by other means in other groups (e.g., insects, fish, and caecilians, respectively). Geoffroy made similar arguments (Appel 1987, 85; Asma 1996, 16).

Owen's argument, however, equally foreclosed the possibility of explaining function in terms of structure. Just as the limbs' functions could not, in virtue of their differences, explain the *sameness* of structure, so too the limbs' shared structure could not explain their *differences* of function. Granted, the differences in structure between the various forelimbs (e.g., the long, thin fingers of the bat compared to the stubby fingers of the mole) might explain their differences in function, but Owen allowed that these modifications of the underlying archetypal pattern were to be explained functionally.