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Origin of the vertebrate body plan via mechanically biased conservation of regular geometrical patterns in the structure of the blastula

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ABSTRACT

We present a plausible account of the origin of the archetypal vertebrate *bauplan*. We offer a theoretical reconstruction of the geometrically regular structure of the blastula resulting from the sequential subdivision of the egg, followed by mechanical deformations of the blastula in subsequent stages of gastrulation. We suggest that the formation of the vertebrate *bauplan* during development, as well as fixation of its variants over the course of evolution, have been constrained and guided by global mechanical biases. Arguably, the role of such biases in directing morphology—though all but neglected in previous accounts of both development and macroevolution—is critical to any substantive explanation for the origin of the archetypal vertebrate *bauplan*. We surmise that the blastula inherently preserves the underlying geometry of the cuboidal array of eight cells produced by the first three cleavages that ultimately define the medial-lateral, dorsal-ventral, and anterior-posterior axes of the future body plan. Through graphical depictions, we demonstrate the formation of principal structures of the vertebrate body via mechanical deformation of predictable geometrical patterns during gastrulation. The descriptive rigor of our model is supported through comparisons with previous characterizations of the embryonic and adult vertebrate *bauplane*. Though speculative, the model addresses the poignant absence in the literature of any plausible account of the origin of vertebrate morphology. A robust solution to the problem of morphogenesis—currently an elusive goal—will only emerge from consideration of both top-down (e.g., the mechanical constraints and geometric properties considered here) and bottom-up (e.g., molecular and mechano-chemical) influences.

Contents

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“*The origin of life, the evolution of increasing biological complexity, and the development of the embryo from a single egg cell, all seem miraculous at first sight, and all remain largely unexplained*.” —Paul Davies

“*The palm will be won by the one who can trace the formative forces of the animal body back to the general forces that direct the life of the universe*.” —Karl Ernst von Baer

1. Introduction

1.1. Animal form: a longstanding problem

Foremost among the unresolved problems confronting modern biology is the origin of biological complexity, most notably that of the shape and form of our own bodies. From Leonardo Da Vinci and Vesalius to Gray's *Anatomy*, anatomists have succeeded in providing detailed descriptions of the musculoskeletal, organ, and nervous systems. Yet, the problem of the origin of these and other aspects of organismal form remains unresolved. Since the body develops from the embryo, nineteenth century anatomists reasonably sought a solution from the observation of early animal development—or embryogenesis. By the end of the nineteenth century, the embryological stages of nearly all major phyla had been characterized in excruciating detail. But no answers were forthcoming, as the form of the embryo seemed to emerge, in a sudden ‘phase shift,’ from a mass of cells, giving no clue as to the mechanism responsible for the organization of that form. Moreover, while there must necessarily be a relationship between the emergence of animal form during somatic development and the advent of new phyla during evolution, the nature of this relationship is still poorly understood. For example, the evolutionary transition from marine tetrapods to land vertebrates was recently illuminated by the discovery of *Tiktaalik roseae* and other transitional forms (Shubin et al., 2006a, 2006b, 2014). Yet, the origin of the earliest fish remains a mystery and we still seek a plausible explanation for the emergence of limbs from fins. Based on morphological similarities, amphioxus, the larval stage of tunicate, and the Cambrian *Pikaia gracilens Walcott* have each been suggested as possible precursors of early fish, though the origins of these forms have not been explained (Morris and Caron, 2012). In another example, Darwin gave a plausible account of the emergence of different beak adaptations among Galapagos finches (Darwin, 1859). Nevertheless, natural selection doesn't provide a mechanism that would explain the advent of diverse beak designs, much less the overall morphology of the members of the tanager family known as Darwin's finches. *On the Origin of Species* doesn't actually address the rise of new species. Rather, it confronts the question of how selection might work, *once myriad variations have been established* (Darwin, 1859). Recent work highlighting the importance of genetic and epigenetic interactions in the evolution of Darwin's finches suggests that neither one nor the other should be considered to have primacy in the emergence of new species (Skinner et al., 2014). The mechanism underlying the origin of radically new forms thus remains very much an open question (for a comprehensive précis of the history and contemporary study of the origin of vertebrate form, see Onai and Kuratani, 2014; for a review of the problem of macroevolution, also see Vrba and Eldredge, 2005).

The description of the conceptual model proposed here is followed by an historical account of the problem of vertebrate form and an outline of relevant scientific and philosophical considerations. The authors beg the reader to suspend skepticism that such a complex and longstanding problem is subject to a solution of relative simplicity. Though neither rigorous nor exhaustive in an empirical sense, our model offers an intuitive and plausible description of the emergence of form via simple geometrical and mechanical forces and constraints. The model provides a template, or roadmap, for further investigation, subject to confirmation (or refutation) by interested researchers.

1.2. Embryo geometry

The body plans of complex organisms are predominantly radially or bilaterally symmetric. Animals with radial symmetry have vase-like bodies. Animals with bilateral symmetry comprise segmented tubes with anterior heads, dorsal eyes, and pairs of jointed and pointed limbs. All complex organisms initially develop from an egg that cleaves alternately along the three spatial axes, yielding eight cells arranged as the corners of a cuboid form. Further divisions create the blastula, a ball of hundreds of cells of fairly regular geometry derived from the earlier cuboid form