



Review

Why are there eggs?



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ABSTRACT

A description and update of the “egg-as-novelty” hypothesis is presented. It is proposed that the major animal phylum-characteristic suites of morphological motifs first emerged more than a half-billion years ago in multicellular aggregates and clusters that did not exhibit an egg-soma divergence. These pre-metazoan bodies were organized by “dynamical patterning modules” (DPMs), physical processes and effects mobilized on the new multicellular scale by ancient conserved genes that came to mediate cell–cell interactions in these clusters. “Proto-eggs” were enlarged cells that through cleavage, or physical confinement by a secreted matrix, served to enforce genomic and genetic homogeneity in the cell clusters arising from them. Enlargement of the founder cell was the occasion for spontaneous intra-egg spatio-temporal organization based on single-cell physiological functions – calcium transients and oscillations, cytoplasmic flows – operating on the larger scale. Ooplasmic segregation by egg-patterning processes, while therefore not due to adaptive responses to external challenges, served as evolutionarily fertile “pre-adaptations” by making the implementation of the later-acting (at the multicellular “morphogenetic stage” of embryogenesis) DPMs more reliable, robust, and defining of sub-phylum morphotypes. This perspective is seen to account for a number of otherwise difficult to understand features of the evolution of development, such as the rapid diversification of biological forms with a conserved genetic toolkit at the dawn of animal evolution, the capability of even obligatory sexual reproducers to propagate vegetatively, and the “embryonic hourglass” of comparative developmental biology.

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1. Introduction

A publication several years ago suggested that the animal egg originated later in evolution than the main morphological features of animal body plans and that it was retained by virtue of its unique capacity to stabilize developmental pathways [1]. The implication of this hypothesis is that while an egg-stage characterizes most present-day animal life cycles, the respective eggs, and

the transient and persistent heterogeneities that appear within them before and after fertilization, play a much more limited role in embryogenesis than would be implied by their position at the initiation of development.

Several puzzles are resolved by this concept, if true. These include the capability of some metazoan organisms to circumvent the egg-stage and develop normally as asexual propagules or monozygotic multiples, the ability of embryo-cell chimeras of phylogenetically divergent members of some phyla, whose development is otherwise egg-dependent, to develop into healthy, though evolutionarily unprecedented, representatives of the

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phylum, and the observation that species within a given phylum can exhibit very different egg types, pass through a common intermediate morphology (the phylotypic stage), only to diverge again, exemplifying the “embryonic hourglass.”

The “egg-as-novelty” hypothesis was based on the earlier recognition that animal development is mediated by physical forces, processes, and effects acting on multicellular clusters [2,3]. These clusters arise part-way during development, and are variously termed (depending on the species) blastula, blastoderm, or inner cell mass. The physical effects that mold and pattern these clusters are mobilized by the products of certain ancient, conserved genes (the “interaction toolkit”; [1]), forming a collection of “dynamical patterning modules” (DPMs). Since different animal clades have different subsets of interaction toolkit (IT) genes, not every DPM is manifested in all embryo types [1,4]. Indeed, it was proposed that the approximately three-dozen animal phyla are defined by their DPMs, which in turn are specified by the presence or absence of the various IT genes [1].

The hypothesis has several components, each with a set of assumptions:

- (i) The distinct metazoan body plans arose in populations of unicellular organisms that were the common ancestors of the present-day multicellular animals and single-celled choanoflagellates. The ancestral cells contained genes (inferred by their presence in descendants) for cadherins and other cell surface proteins. These molecules acquired homophilic adhesive properties at some point, giving the cells the capability to aggregate.
- (ii) The ancestral cells also contained a selection of additional IT genes, so when a critical cell number was reached in the aggregates, combinations of DPMs were brought into play and primitive versions of phylotypic body plans took form. (The species-characteristic cluster of dozens to hundreds of equal-sized cells at which this occurred is termed the “morphogenetic stage” [1].) The cells of these populations, while generally uniform regarding their complements of IT genes, were otherwise genetically variable.
- (iii) Cells in these ancient aggregates had, it was argued, less stringent size regulation than present day cells. “Proto-eggs” were cells in these aggregating populations that were larger than typical. When released from an aggregate and induced to divide, their large size was an impediment to complete cytokinesis. This had the effect of producing morphogenetic-stage clusters in which the cells were clonal and thus of uniform genotype. These clusters were the first *multicellular individuals*, and were new units of selection. Alternatively, proto-eggs that produced a confining matrix – a primitive zona pellucida – would foster non-dispersal of daughter cells, and thus clonal cell clusters, even if not produced by cleavage.
- (iv) The interiors of proto-eggs were loci of a variety of “egg-patterning processes” (EPPs). These derived from previously established physiological phenomena in single cells – calcium ion transients and oscillations, cytoplasmic flows – that came to operate at a larger scale than that of the cells in which they had originally functioned. The effect of EPPs was to cause the egg cytoplasm to become spatially nonuniform, and this, in turn, led to morphogenetic stages in which different cells (despite being genetically identical) had different molecular compositions.
- (v) EPPs, therefore, were not *adaptations*, i.e., phenotypic characters that arose by natural selection in response to external challenges, but rather side-effects [5] or “spandrels” [6], inexorable consequences of other changes (in this case, enlargement of the founder cell), with indeterminate evolutionary consequences.

- (vi) The phylum-associated DPMs that were subsequently (at the embryo’s morphogenetic stage) mobilized in cell clusters earlier acted upon by EPPs were implemented with pre-set boundary and initial conditions, making their morphological outcomes more reliable and stereotypical than they would be with random starting conditions. Furthermore, because cell clusters of a given phylotype (i.e., multicellular individuals with a phylum-characteristic array of IT genes) could sustain different EPPs and therefore generate distinct spatially nonuniform morphological-stage spatiotemporal patterns, stable subclades (subphyla, classes, and so forth) could arise within each phylum. In this sense, EPPs were often pre-adaptations or “exaptations” [7] that ultimately contributed to stability and diversification of taxonomic identity.

This scenario for the origination of eggs implies that true eggs were late arrivals in the evolution of animal development. They would have arisen over time from proto-eggs, which themselves succeeded the emergence of the characteristic morphological motifs of the Metazoa. Following the appearance of proto-eggs, the evolution of oogenesis, i.e., the pre-release specialization of these organism-founding cells, including introduction of maternal factors, would have prepared them for increasingly determinate and reliable transformation by subsequently activated EPPs. Such activation could (at different evolutionary time points), have been spontaneous, caused by specific environmental cues or by other specialized cells, proto- and definitive male gametes. This implies that the egg cell had an independent evolutionary path from the sperm cell and from sexual differentiation itself.

My objective here is to establish the plausibility that all animal body plans, even those that in present-day forms obligatorily arise from sexual reproduction, were primitively independent of an egg stage. In the absence of experimental access to extinct organisms, the most decisive tests of this hypothesis are those that relate to the autonomy, in extant organisms, of multicellular development from any process involving an egg, or where that is not possible to demonstrate, of the establishment of the major phylum-specific features of body plans independently of the details of pre- or post-fertilization intra-egg patterning. Such findings would be most persuasive if independence from the egg could be demonstrated in situations never plausibly encountered in phylogeny, and therefore representing primitive capabilities rather than evolved mechanisms compensating for developmental perturbation. The following section contains several such examples.

2. Evidence for the egg-as-novelty hypothesis

2.1. Eggs are not needed for complex, multicellular development

In a critique of “adultocentric” concepts of development, the evolutionary-developmental biologist Alessandro Minelli provides numerous examples of organisms whose development does not begin with, or pass through, an egg stage [8]. Marine and freshwater sponges, as well as colonial cnidarians such as corals, release multicellular propagules which develop into organisms indistinguishable from the originating ones [9]. Other cnidarians, such as members of the freshwater genus *Hydra*, reproduce instead by an intraorganismal vegetative process. These small, tubular animals produce featureless buds that extend laterally from the body stalk. The primordium develops in an apicobasal sequence into a fully mature individual before detaching from the parental organism at its newly formed basal disc, the last structure to differentiate [10].

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