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EDITORIAL

JEZ-B MOLECULAR AND DEVELOPMENTAL EVOLUTION WILEY

# *JEZB* special issue on eggs

In this special issue, we invite you to consider the broad concept of "the egg," which in turn is simply one form of the single-celled propagule stage, or gamete, of multicellular organisms. The articles in this special issue consider "the egg" from a variety of perspectives, from the theoretical to the experimental, encompassing a wide variety of biological subdisciplines.

The word "egg" means different things to different biologists. Depending on the subfield of biology where one specializes, the word egg can take on different connotations. For ornithologists, for example, it evokes a familiar shape that can be held in a hand, perhaps with charismatic patterning and obvious ecological importance. For biologists who focus on other animals, the notion of an "egg" often blends smoothly into ideas of a developing embryo. And in some areas of specialization, such as plants or fungi, the idea of an "egg" might not seem particularly relevant at all.

Here we use the term "egg" as a starting point to consider potential higher-level features that unite "the egg" across multicellular organisms: that is, the single-cell stage that multicellular organisms pass through during their life cycles. Thus conceived, we are considering the many forms that this single-cell stage takes, including gametes and single-celled embryos. We have brought together original primary research and synthetic reviews that represent a diverse array of perspectives on these single-celled stages, including bird and insect eggs, sperm, and pollen. The special issue concludes with a consideration of the developmental and evolutionary origin of gametes.

We hope that readers will appreciate, as we do, how studying this single-cell stage highlights the interplay of multiple levels of biological and evolutionary organization. The single-cell stage can be studied as an individual organism that interacts with its environment, as a vehicle for studying behavioral evolution, as an arena for studying the specific function of individual genes, as a tissue exhibiting emergent biological pattern formation, or as the terminus of a cell-type specification cascade. Collectively, the research presented in this collection draws on and contributes to multiple fields including behavioral ecology, organismal evolution, cell physiology, developmental genetics, biochemistry, protein evolution, and developmental biology.

Contributions from the *Stoddard* and *Rezende* groups consider the single-celled stage as a stand-alone, distinct individual interacting with other organisms and the environment. These are examples where the research focuses on functional traits that develop in the larger ("female") gamete, yet only become pertinent after the egg has been fertilized and laid. Quach et al. use the eggshells of seabirds to present evidence the single-celled stage is visually patterned in a way that is pertinent for the behavior of adult individuals. The eggshells of these birds have complex pigmented patterns, which the authors quantify to assess the visual information that is accessible to the adults of four different species. Vargas et al. also consider eggshell traits, but in this instance, the traits are secreted structural features that confer resistance to desiccation for the developing embryo. They provide data suggesting that in insect relatives called springtails, the materials provided by the adult female during oogenesis are not sufficient to protect the embryo. The embryo itself adds an additional layer to the eggshell, which plays a crucial role keeping the egg from drying out.

Considering the smaller ("male") gamete, work from the *Mainer* and *Radja* groups research highlights how proteins function in the cellular biology of the single-celled stage, ultimately generating morphological diversity. Chebbo et al. use *Drosophila* sperm as a study system, building on previous work from their group and others showing that these cells are morphologically variable across taxa, and that their shapes are also under strong selection. Focusing on a gene that is rapidly evolving in *Drosophila*, they provide evidence for its role in the length of the sperm tail length, with counterintuitive effects on male and female fecundity. Radja considers a single-celled stage of flowering plants —pollen—that is morphologically variable across taxa, but where in contrast to *Drosophila*, we are only beginning to understand the cell biological underpinnings of shape. Her review summarizes the state of the field of observing and modeling pollen formation, with suggestions for promising future avenues.

Two of the papers in the collection then go on to consider the process of gamete fusion, from the perspective of plants (*Kawashima* group) and animals (*Swanson* group). At fertilization, two different single-cell cell-types join together with a series of specific steps that ultimately result in a successfully developing embryo. Shin et al. address the fertilization of flowering plants, wherein two sperm cells fuse with two female gamete cells. Their review touches on the cellular and molecular basis of this apparently unique form of fertilization, with some comparisons to features of animal fertilization. Carlisle and Swanson consider the analogous process in animals: when a sperm meets an egg, "gamete recognition proteins" mediate the initial interaction between the two cell types. Their review covers what is known about these proteins and their evolution, with a discussion on how the coevolution of these proteins contributes to barriers to hybridization.

Finally, *Wessel* and *Rose* put all of these issues in broad evolutionary context, by considering the developmental and evolutionary origins of the single-cell type. Wessel et al. explain that during animal development, gametes are typically understood as being derived from "the germ line," a lineage of cells that is specified fairly early in embryogenesis. Their review covers recent evidence that in some animal species gametes can be formed from tissues that were not set aside as early as in the embryos of the best-studied animal model species, nor continuously maintained as a totipotent pool of regenerative cells. Caroline Rose takes a bird's eye view of the emergence of reproductive division of labor at the cellular level. She discusses options for the evolutionary sequence of events that gave rise to multicellularity—and by extension, the single-celled stage of multicellular organisms. Her review and perspective piece addresses this ongoing debate, and advances the hypothesis that the emergence of specialized reproductive cells (i.e., a "germ line") was a crucial precursor to the subsequent emergence of obligate multicellularity.

In conclusion, our hope is that publishing this collection of papers together within one special issue, will encourage readers to read them alongside one another. A major challenge presented by the study of single cell stages, is that our different frameworks for studying nature (genetic, cellular, organismal, morphological, etc.) are brought together, intersecting at a single time and structure in the life cycle. We hope that these articles will in turn give rise to further insights in other systems.

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