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Editorial: MorphoEvoDevo: a multilevel approach to elucidate the evolution of metazoan organ systems

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Editorial on the Research Topic
MorphoEvoDevo: a multilevel approach to elucidate the evolution of metazoan organ systems

1 Introduction

The evolution of animal morphologies has been a preoccupation of biologists at least since the XVIII century, when comparative methods were first used to model the transformations of animal form over evolutionary time. This relevance was encapsulated in Darwin's dictum: "Morphology [is] the most interesting department of natural history, [which] may be said to be its very soul" (page 434 of *On the Origin of Species*). Morphology, understood as a hierarchical construct (from molecules to cells, organs, and individuals), is still the central focus of the new field of EvoDevo.

Over the last 15 years, the International Society for Invertebrate Morphology (ISIM) has been meeting regularly to discuss the most current issues in the field. We have witnessed the incorporation of powerful technologies (i.e., single-cell RNA sequencing (scRNA-seq), serial transmission electron microscopy (TEM), and genomics), enabling the study of older problems in a new light. Moreover, the analysis of structures and processes now involves gathering data at different levels of complexity, from transcripts through cell types, tissues, and organs to whole bodies. With the help of phylogenetics and paleontology, the scales of our analyses have both spatial and temporal components. Integrating these data leads us to a more comprehensive study of morphology and easy movement across different scales, a prominent characteristic of presentations at past and present International Congress on Invertebrate Morphology (ICIM) meetings. The last of these, ICIM5, took place in Vienna between the 8th and 12th of August, 2022, and was organized by one of us (Andreas Wanninger). The presentations, ranging from the genomic control of development to cell lineage specification as well as the architecture and function of tissues and organs, showcased a variety of intellectual and methodological approaches that attested to our community's vibrant activities. Accordingly, ICIM5 embraced a wide field of research areas as is reflected in the meeting's following core topics: MorphovoDevo; Functional Morphology; Molecular Basis of Morphological Diversity; Morphology in Deep Time; Morphology, Integrative Taxonomy and Phylogeny; Senses, Neurons and Behavior; Technological Advances in Microscopy and Imaging; Evolution of Multicellularity.

Some of these contributions, but also work that has not been presented at ICIM5 including studies on vertebrates, are included in this Research Topic entitled "MorphoEvoDevo: A Multilevel Approach to Elucidate the Evolution of Metazoan Organ Systems." We thank all colleagues who presented and shared their data and participated in the vital discussions on various topics of animal morphology, function, and evolution during ICIM5, 2022, and to those who contributed to this Research Topic. In the following, we summarize the essence of the papers published herein, grouping them by subject. Papers are bundled together based on the major level of analysis used, thereby being aware that they often tackle similar problems at different scales, an approach that we very much encourage (see also the final discussion for a critical assessment of the state of the field).

2 Genomes, transcriptomes, phylogeny: from single genes to gene collectives

As sequencing technologies and methods improve, the number and taxonomic coverage of sequenced genomes and transcriptomes continue to increase. Paps et al. discuss how these advances have informed our hypotheses of major evolutionary events within animals and plants such as the origin of multicellularity, and what challenges, such as poor taxon sampling, still remain. The authors compare evolutionary transitions in metazoans with those that occurred in plants, highlighting the multiple versus single origins of multicellularity, respectively, evolution of genomic novelty, and adaptations to terrestrial life. Genomic novelty in plants has been previously linked to the activity of transposable elements, and in this issue, Mukherjee and Moroz demonstrate the convergent generation of clusters of new transcription factors by transposable elements across different metazoan clades including *Hydra*, annelids, and mollusks (cephalopods, oysters, and sea slugs). Within Metazoa, there are abundant examples of morphological innovations, and comparative scRNA-seq is beginning to help us unravel the origins of these novelties. One morphological novelty that has long been studied is the molluscan shell. Salamanca-Díaz et al. compared the genetic toolkit for shell formation (embryonic shell or protoconch I and larval shell or protoconch II) in a conchiferan, the invasive quagga mussel *Dreissena rostriformis*, by generating single-cell transcriptomes for embryonic and larval cells. They found significant differences between gene complements across the two developmental stages as well as many novel genes with no clear ortholog, bringing into question the homology of the shell field across life history stages within a species and across molluscan taxa. Continued integration of phylogenomics, comparative genomics, and single-cell transcriptomics will enable us to continue answering questions surrounding the origins and diversification of major taxonomic clades and their morphological properties, providing insight into how multicellular life evolved.

3 Cellular and tissue diversity of animals

With the recent establishment of scRNA-seq, evolutionary biologists have now a tool at hand that allows for comparative analysis of gene expression signatures of individual cells or tissues of animals, thereby grouping them into so-called clusters and trajectories. Depending on how distinct the expression profile of a given cell cluster is from others, individual cell types that express key marker genes may be defined. If used in a comparative context across species, novel hypotheses on putative cell type homologies may be formulated. In order to facilitate such studies, Paganos et al. have established an easy-to-use method (whole animal freeze-fracture scanning electron microscopy; WAFFSEM), where small marine animals (embryos, larvae) are processed in such a way that cell types can be readily identified by scanning electron microscopy. They argue that a combination of their technique and other microscopic and molecular tools such as scRNA-seq will facilitate such comparative cell type analyses. Following their own rationale, a second paper of this group (Paganos et al.) combines serial block-face scanning electron microscopy and scRNA-seq to characterize pancreatic cells in developing sea urchins. They found that the sea urchin exocrine pancreas-like cells are molecularly and morphologically distinct from other cell types of the digestive tract and propose homology between these and the pancreatic cell of mammals, implying that such a cell type was already present in the last common deuterostome ancestor. Moroz and Romanova use a combination of morphological and scRNA-seq data in order to tackle the long-standing question about the identity and homology of neurons. They argue that neurons and synapses evolved multiple times independently in the animal tree of life and that nervous systems comprise different, non-homologous cell types. Using hemichordates as models for comparative research into genes that govern animal regeneration, Humphreys et al. found that these deuterostomes, during head regeneration, express genes that are closely related to those used by regenerating planarian flatworms and the cnidarian *Hydra*. These "stem cell reprogramming factors" appear to also be present in mammalian cells, although these animals do not show extensive regeneration abilities, raising the question as to what underlying mechanisms trigger the activation of these regeneration circuits in hemichordates.

In their quest to identify and characterize the expression profiles of cells that contribute to the tissues that form distinct morphological features in mollusks, such as the shell, foot, and neuromuscular systems, Salamanca-Díaz et al. provide a detailed atlas that identifies cell clusters in the trochophore larva of a bivalve mollusk using scRNA-seq. The developmental trajectories of cells were traced, resulting in the reconstruction of the common origin of cells, e.g., from ectodermal precursors. Identified marker genes for each cell cluster were used to test for their *in situ* expression patterns in the respective stages of the developing bivalve. The data provided show that the identified cell populations indeed contribute to distinct morphological features, thus providing an important framework for future comparative cell genealogical studies into mollusks and other lophotrochozoans.

4 The architecture of animal tissues

Both gene expression as well as cellular and tissue dynamics during morphogenesis have long been used to infer the nature and evolutionary trajectories of key animal features such tissues or organs. In vertebrates, *Pax3/7* genes regulate the closure and patterning of the neural tube. Extending these studies to tunicates by using gene expression and CRISPR/Cas9-mediated mutagenesis, Kim et al. found that this is also the case in the model tunicate *Ciona*, suggesting that this key function of *Pax3/7* was already present in the last common vertebrate-tunicate ancestor. Neural crest and craniofacial development are two additional classical fields of research that have entered a new era by incorporating novel molecular tools into their research programs. In his topical review, Newton explores the possibilities of including “comparative evo-devo-omics” into assessing how different phenotypes are established during vertebrate development, in particular with respect to facial morphology. Thereby, he introduces the fat-tailed dunnart as a new marsupial model that, by comparing its developmental patterns with those known from mouse, should allow us to discern conserved from species-specific processes that generate craniofacial variation in mammals. Hampl et al. focus on another cranial component of vertebrates, the secondary palate, that in mammals forms a bony plate separating nose and mouth from each other. While in mammals two shelves are formed that subsequently fuse in the midline, development of these shelves varies considerably among reptile species ranging from open to fully closed phenotypes. The authors found that in chameleons the secondary palate closes after hatching. They identified various molecular factors that play a role in the growth of the palatal shelves and discuss variation in palate formation among amniotes.

Moving away from cranial hard part development, Macrì and Di-Poi studied cerebellar development in a lizard and a snake in order to assess differences of brain subdivision among vertebrates. They found that ontogenetic processes that were thought to be constrained to birds and mammals are also at play during cerebellogenesis in squamates, and that heterochronic shifts most likely influence mechanisms of molecular interactions between neural cell types in snakes. Painting an even bigger picture of neural evolution, Martinez and Sprecher ask the question about the factors that have allowed for the evolution of complex, centralized neural systems (brains, or “central processing units”, CPUs, as they call them). They propose a scenario where, in a first step, receptors and then, in their proximity, neurons evolved, that were capable of transmitting signals. In areas with condensed neurons, the production of additional receptors was promoted, thus increasing signal processing in these areas (e.g., anteriorly in a prospective “head”). The increased presence of receptors would in turn have stimulated further neuron production, thereby generating a positive feedback loop that provided the prerequisite for shaping the vast amount of distinct neuronal phenotypes in the animal kingdom.

Not only skeleto- and neurogenetic processes but virtually all developmental pathways are highly dynamic. This becomes obvious if seemingly simple systems (e.g., at early ontogenetic stages that only comprise a few dozen or so cells) are studied. Zieger et al. looked into this phenomenon by analyzing intercellular lumen formation that is crucial for osmoregulation during early embryonic stages in the freshwater bivalve *Dreissena*. Their study showed that the water channel protein aquaporin is only associated with the midbody, a structure that is part of the intercellular cytokinetic bridge that is crucial for lumen formation. The direction of cavity expansion during cleavage depends on the location of the aquaporin-bearing midbodies, and if the microtubules that form the cytokinetic bridge are disrupted, no lumen is formed. Such embryos are incapable of expelling excess inflowing water and thus of osmoregulation. Since lumen formation during cleavage is a widely known phenomenon in freshwater invertebrates, the authors hypothesize that the mechanism they found in *Dreissena* may be widespread among such animals.

5 Animal organs and body parts: identity, variation, and evolution

The nature and function of animal organ systems and body regions has been a key topic in zoological research for centuries. In his review, Minelli outlines how the study of organs and body parts has changed over the past 200 years. While earlier morphologists either defined organs based on their very structure (morphology) or their function, today’s evolutionary biologists incorporate the developmental mechanisms by which these structures are formed during ontogeny, thereby including morphogenetic, molecular, as well as cell type composition in their analyses. However, using the evolution of hermaphroditism as an example, Minelli argues that a sharp distinction between a morphological- and functional-based definition is vital when assessing the evolutionary pathways of respective body plan features in given animal lineages.

In order to reconstruct the evolutionary origin of the novel mammalian jaw joint, Anthwal and Tucker compared its development in the mouse and the tooth-less monotremes. They found that during platypus and echidna development a fibrocartilage disc primordium is formed, a structure that is associated with the mammalian jaw joint. However, this disc is not fully formed in the monotremes and resembles a state similar to that in mutagenic mice with reduced overall cranial musculature, leading the authors to conclude that the monotreme situation is due to a secondary loss of the jaw joint disc and dentition, and that the last common ancestor of Mammalia did carry teeth.

6 Fossils and development as windows into the evolutionary past: changing morphologies and ontogenetic strategies over time

The three papers of this topic ideally illustrate that both paleontology and developmental studies provide important insights as to how organisms or individual traits may have evolved over evolutionary time. In their study on the morphology, function, and replacement of teeth in the common Triassic sauropterygian *Keichosaurus*, Liao et al. used thin sectioning and X-ray computed microtomography. By comparing their findings to those on recent and Paleozoic piscivore vertebrates, they conclude that *Keichosaurus* likely fed on small fish and soft body invertebrates such as shrimps. At a branch of the animal tree of life far distant to the vertebrates are the placozoans, seemingly simple-built multicellular creatures without distinct neurons, muscles, or body axes. Employing long-term culturing of these "pre-bilaterians", Romanova et al. found that in addition to the well-known asexual reproductive strategies by fission and the production of ciliated swarmers, placozoans may also use the epithelial spheres to produce juvenile offspring. The diverse modes of asexual reproduction in placozoans prompts the authors to suggest these animals as potentially suitable experimental models for research into animal regeneration.

On a more theoretical side of evolutionary biology, Martynov et al. revisits the linkage of ontogeny and phylogeny by elaborating on traditional concepts such as Ernst Haeckel's biogenetic law ("ontogeny recapitulates phylogeny") or the hypothesis of a conserved phylotypic stage for given animal lineages. They argue that ontogeny is not only a result of phylogeny, but instead generates animal diversity through variations introduced during evolution, thereby affecting the (adult morphological) phenotype. As such, it should be possible to infer phylogenetic relationships using ontogenetic data, and the authors propose "ontogenetic systematics" as a crucial discipline in biology. According to them, this also requires a refined definition of the often interchangeably used terms "paedomorphosis", "neoteny", and "progenesis".

7 The future of MorphoEvoDevo

The contributions to this Research Topic demonstrate not just the vitality of the field but also the analytical complexity that contemporary investigators require to understand the evolution of morphologies. This is a field that lies at the intersection of different disciplines, from molecular genomics to morphological comparisons and paleontology. To a large extent, it still relies on the use of comparative methods and extrapolation from well-understood datasets. The fact that most evolutionary transitions occurred over long, hidden periods of time make some of these extrapolations rather difficult, if not far-flung. Ideas about the origin of key taxa and morphological innovations such as metazoans, bilaterians, brains, and mesoderm, are hinted at, at best. The scenarios proposed are undoubtedly based on inferences but, more and more, on well-informed ones. Data gathered by the new technologies—including genomics, scRNA-seq, knockdown technologies, and spatial transcriptomics—are helping us to dissect developmental processes with unprecedented detail, providing valuable data to revisit the diverse (old and new) evolutionary hypotheses. In addition, the recent incorporation and refinement of phylogenetic methods improve the understanding of highly debated clade affinities and, thus, permit more informed predictions of how morphological changes might have happened over evolutionary time.

But this is, perhaps, still a rosy picture. We noticed—particularly during the meeting but also reflected in these papers—that there remains room for improvement. Single-cell data (identification of cell types and subtypes) still lack proper resolution in most invertebrates. Moreover, the cross-species comparison and identification of cell type homologies is in its infancy; it is still challenging to infer the evolutionary history of cell types across animal groups. The cell atlases need to be transformed into cell maps of whole animals, specifying where all those identified cell types reside in the animal body. We also need to know how these cell types are organized into tissues. Clear progress has been made in mapping the positions of cell types, mainly in the context of high-throughput TEM reconstructions (e.g., connectomics). However, these approaches are still limited to very few animals. Highly automated systems in electron microscopy (i.e., serial block face scanning, etc.) are paving the way to more extensive analyses of tissue architectures. Needless to say, these maps should represent a broad taxonomic range; otherwise, transformations of tissues in evolutionary time are difficult to trace and will remain highly speculative. Genomics seems to be an area of fast progress, primarily due to the reduced costs of sequencing and increased computational power. A flurry of papers, plus huge sequencing projects (e.g., Earth Biogenome), are spearheading a bloom of comparative genome studies. Such advances have been complemented recently with the exploration, via epigenetic analysis, of the response of whole genomes to processes such as development and regeneration. Again, while this is encouraging, the transition from accumulating tons of data to distilling critical biological information is still wanting. The idea that huge datasets per se can inform us directly about specific biological processes is still a sign of over-optimism. More needs to be done to bridge these levels.

One relevant consequence of genome analysis and the use of technologies in the molecular realm is the development of functional assays. In the last decade, the introduction of CRISPR technologies (plus the extension of RNAi methods) has allowed us to analyze gene function in several animals and developmental contexts. We have moved from speculation about gene function (primarily based on homologies or just *in situ* patterns) to evaluating these functions *in vivo*. In addition, the generation of transgenic animals, a necessary complementary tool, is a pressing need. These methods are promising but need to be implemented in more animal systems and at a larger scale; otherwise, deciphering complex gene regulatory networks would need some time.

While the above-described use of new technologies has illuminated speculations on the origin of morphological and molecular novelties, we should not forget that the path leading to a specific morphological transition can best be directly evaluated by searching for appropriate fossils, the only real transitional forms (maybe with the sole exception of ontogenetic sequences of morphogenesis that may provide a window into the evolutionary past and relatedness of organisms). Without a proper investigation of the fossil record, our scenarios lack a solid testing ground. More and more fossils corresponding to critical transitional periods (i.e., Precambrian-Cambrian) have been unearthed during the last few decades. This is particularly interesting, given that most of these deposits have revealed previously unimagined transitional forms, forcing us to reconsider evolutionary trajectories.

All in all, we believe that investment in emerging technologies and expansion of the phylogenetic range of our analyses open up the field of MorphoEvoDevo to a bright future. Integrating knowledge gathered across different scales should be a clear objective for the near future, since it is only by moving between them that we can suggest solid (informed) scenarios for the evolution of morphologies. Those at ICIM5 have witnessed a clear movement in this direction, and we anticipate that the following meetings will bring many new surprises to the field. On a particularly positive side of things, we believe that the diverse assemblage of contributions at ICIM5 and in the present Research Topic of Frontiers in Ecology and Evolution, that all identify themselves as revolving around animal morphology in the broadest sense, clearly demonstrates that we are about to overcome the long-standing methods-based rivalry between “morphologists” and “molecular biologists”. More and more evolutionary zoologists are using methods just the way one should: as undogmatic tools to answer important questions. In doing so, we should get closer to describing biological reality more accurately as more suitable technologies are employed—often in form of larger collaborations where individual partners contribute their expertise to joint research programs.

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