Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Insect Science

Editorial Overview: Development, regulation and evolution of organ systems

Cassandra G Extavour and Leslie Pick

Current Opinion in Insect Science 2016, **13**:vii–ix

For a complete overview see the Issue

Available online 5th March 2016

http://dx.doi.org/10.1016/j.cois.2016.03.005

Cassandra G Extavour[1,2]

[1] Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, United States[2] Department of Molecular and Cellular Biology, Harvard University, Cambridge, MA 02138, United States

Cassandra Extavour is Professor of the Department of Organismic and Evolutionary Biology, and of the Department of Molecular and Cellular Biology at Harvard University. She received her B.Sc. from the University of Toronto, her Ph.D. from the autonomous University of Madrid, and did postdoctoral work with Michalis Averof in Crete, Greece and with Michael Akam in Cambridge, England. She studies the evolution of molecular mechanisms that control separation of germ line and soma, using arthropods as model systems.

Leslie Pick

Department of Entomology, University of Maryland, College Park, MD 20742, United States
e-mail: lpick@umd.edu

This special issue on Development, Regulation and Evolution of Organ systems highlights recent findings using insect model systems to probe this important topic. Much of the basic research done with insects over the past ~100 years has focused on the fruit fly, *Drosophila melanogaster*, for which an enormous wealth of information has been obtained. This work on *Drosophila*, from classical genetics to genomics, guides many studies in other insects both from its use as a resource and as a point of comparison. Although work on *Drosophila* has yielded many valuable insights into the developmental and molecular mechanisms regulating organ formation and function, given the highly derived nature of *Drosophila* development, understanding organ system evolution requires extending these studies to additional insect models. The availability of large amounts of data on genes and gene function in *Drosophila* allows researchers to hone in on candidate gene families and regulatory networks when exploring related processes in divergent taxa. The collected articles in this issue share a comparative focus and address the development and regulation of different organ systems, with particular emphases on key evolutionary innovations.

Friedrich et al. use just the type of comparative approach mentioned above to analyze the evolution of regulatory mechanisms controlling the development of the arthropod compound eye. Starting with transcription factors that have well-known roles in controlling photoreceptor differentiation in the *Drosophila* eye, they analyze recent data on these genes in phylogenetically distant arthropod species and propose a model for the evolution of photoreceptor subtypes based on these results.

Clark-Hachtel and Tomoyasu investigate the evolutionary origin of the insect wing, another organ that has been studied extensively in *Drosophila* and which stands as a major model for studies of morphological innovation. These authors review historical discussions about the evolutionary origins of the insect wing. They then go on to analyze more recent functional studies in *Tribolium*, a developing model insect species, and a number of other arthropods. These studies, as above, were initiated on the basis of identification in *Drosophila* of regulatory genes involved in wing and appendage development. However, the novel phenotypes found in other insects lead the authors to propose a dual origin for wing development resulting from the merger of two unrelated tissue types in insect ancestors.

Schmidt-Ott and Kwan review the role of extraembryonic membranes (serosa, amnion, and yolk sac) in insects and discuss recent evidence that these membranes play not only structural roles, but also active roles in the

Leslie Pick is Professor and Chair of the Department of Entomology at the University of Maryland. She received her B.A. from Wesleyan University, her Ph.D. from Albert Einstein College of Medicine and did postdoctoral work with Walter Gehring in Basel, Switzerland. She studies the function and evolution of genes that control embryonic development, using insects as model systems.

morphogenesis and physiology of the embryo. This review highlights the fact that extensive work on this issue in *Drosophila* may provide an exception rather than a rule, as the extraembryonic membranes of *Drosophila* are greatly reduced compared to those of other insects. Recent comparative studies in other flies, beetles and true bugs reveal differential roles for these membranes in distinct stages of early embryonic development for these insects. These studies also suggest that conserved transcription factors and signaling molecules, shared with *Drosophila*, may have changed during evolution to take on modified roles in different taxa.

Through two articles in this issue, one by Brisson and Davis and another by Corona *et al.*, mechanisms underlying polyphenism and phenotypic plasticity in insects are explored. In these cases, the determining events for organ development are not purely genetic, as animals with the same genotype develop differently in response to different environmental cues. Polyphenism as such has not been observed in *Drosophila*, which do not produce 'alternate morphs' seen in other species such as ants, beetles, aphids, bees and others, as discussed in this issue. Despite this, many of the genetic pathways implicated in polyphenisms involve genes well studied in *Drosophila*, as explained by Corona et al. in their analysis of the phenotypic plasticity seen in social insects. In addition, Brisson and Davis emphasize interactions between hormonal and transcriptomic approaches that are apt to reveal novel mechanisms, particularly those involving interactions between sensing of the environment and response to these differential clues. Finally, recent studies implicate important roles for epigenetic changes in plasticity, a topic that will undoubtedly receive more attention in the future.

An important parameter in the development and evolution of diverse body plans of insects is that of allometry, or relative scaling of bodies and body parts. Mirth *et al.* address this important issue in their article, which summarizes the problem and focuses on allometry from a developmental point of view. Pointing out that allometry is often considered from a population level, the authors explain that examining the developmental mechanisms that underpin the regulation of relative or fixed organ sizes has led to new insights in this field, and should remain a priority for future research. They further suggest that information gained via this developmental approach will be necessary to understand how different environments can change allometry in some organisms and organs, but not others. Finally, they point out that developmental and ecological data will prove most fruitful when combined with the tools and perspectives of population genetics, providing a clear trajectory for future work in this area.

Establishment of organs of appropriate size is clearly critical for survival, but equally important is the correct functioning of these organs. Arguably one of the most important organ systems for species survival and evolution is the reproductive system. Two articles in this issue deal with the insect reproductive system. Quan and Lynch take the perspective of considering the initial establishment of gametogenic precursors, the primordial germ cells, during embryogenesis. Looking at reproduction from the other end of the germ cell cycle, an article by Heifetz discusses the response of the female reproductive system as a whole to the mating process. Through these two articles, we learn that on the one hand, while it is clear that different insect embryos use different developmental mechanisms to establish the germ line, the evolution of the molecules that control this process remains largely unexplored. On the other hand, while recent advances in *Drosophila* are starting to uncover the reproductive system's response at the molecular

level, we know relatively little about the anatomical and molecular variations in this process that likely exist across insects.

Taken together, the collection of articles in this special issue highlight three major points that we believe should encourage current and future researchers to exploit insects as model systems. First, insects display arguably the broadest range of morphological, behavioral, and life history traits of any animal phylum. Insects are among the only animal taxa to colonize terrestrial, aquatic and aerial habitats. They can display solitary, primitively social or highly complex obligatorily social life styles, with complex caste systems and polyphenisms that can be heritable, environmentally induced, or both. Their reproductive capacities can vary over three orders of magnitude across insect orders, and their adult life spans can vary from hours to decades. Phylogenomics has recently offered an unprecedented level of certainty in the phylogenetic relationships across insect orders [1], so that it is possible to generate well-supported hypotheses about the evolutionary trajectory of traits of interest.

Second, insects are often easy to rear as large, rapidly reproducing populations in captivity. Especially for terrestrial insects, their embryos are usually deposited externally and can be reared successfully in isolation from the parents, making them amenable to manipulation. Genome editing, RNA interference and other techniques for altering gene function have been successfully applied to an increasing number of insect species. These practical considerations make this group a compelling choice for functional studies of the genetic basis of organ system evolution.

Finally, it is clear that each of the different systems presented in this special issue has typically been studied with a different set of approaches: developmental genetics approaches have tended to dominate studies of the visual system, wings and primordial germ cells; physiology, transcriptomics, and more recently epigenetics, are common tools of choice in the study of polyphenisms, plasticity, and mating response, while population approaches to allometry are only recently being combined with developmental genetics. We suggest that to make new advances in answering the outstanding questions in each of these areas, approaches traditionally limited to one area should be increasingly applied to the others. For example, as highlighted by Mirth *et al.*, future advances in understanding allometry are likely to come from merging developmental and population genetics. Similarly, applying population genetics to the problems of germ cell origins and reproductive organ function, could shed new light on what impact variations in reproductive systems have on genome evolution, and thus on the evolutionary process. Comparative physiology applied to the evolution of wing and eye development could help us understand the functional and potential fitness implications of the wide variety of morphologies displayed by these organs across insects. We encourage the reader to enjoy these articles with these points in mind, and hope that these articles will be both informative and a source of ideas and inspiration for future work.

Acknowledgment

The authors were supported by grants from the National Science Foundation (C.G.E., IOS-1257217) and the National Institutes of Health (L.P., R01GM113230).

References

1. Misof B, Liu S, Meusemann K, Peters RS, Donath A, Mayer C, Frandsen PB, Ware J, Flouri T, Beutel RG, Niehuis O, Petersen M, Izquierdo-Carrasco F, Wappler T, Rust J, Aberer AJ, Aspock U, Aspock H, Bartel D, Blanke A, Berger S, Bohm A, Buckley TR, Calcott B, Chen J, Friedrich F, Fukui M, Fujita M, Greve C, Grobe P, Gu S, Huang Y, Jermiin LS, Kawahara AY, Krogmann L, Kubiak M, Lanfear R, Letsch H, Li Y, Li Z, Li J, Lu H, Machida R, Mashimo Y, Kapli P, McKenna DD, Meng G, Nakagaki Y, Navarrete-Heredia JL, Ott M, Ou Y, Pass G, Podsiadlowski L, Pohl H, von Reumont BM, Schutte K, Sekiya K, Shimizu S, Slipinski A, Stamatakis A, Song W, Su X, Szucsich NU, Tan M, Tan X, Tang M, Tang J, Timelthaler G, Tomizuka S, Trautwein M, Tong X, Uchifune T, Walzl MG, Wiegmann BM, Wilbrandt J, Wipfler B, Wong TK, Wu Q, Wu G, Xie Y, Yang S, Yang Q, Yeates DK, Yoshizawa K, Zhang Q, Zhang R, Zhang W, Zhang Y, Zhao J, Zhou C, Zhou L, Ziesmann T, Zou S, Li Y, Xu X, Zhang Y, Yang H, Wang J, Wang J, Kjer KM, Zhou X: **Phylogenomics resolves the timing and pattern of insect evolution**. *Science* 2014, **346**:763-767.