

The future of Evo-Devo: the inaugural meeting of the Pan American Society for evolutionary developmental biology

Maryna P. Lesoway^{a,b,*}

^a Department of Biology, McGill University, 1205 Avenue Dr Penfield, Montreal, QC, Canada H3A-1B1

^b Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Ancon, Republic of Panama

*Author for correspondence (e-mail: maryna.lesoway@mail.mcgill.ca)

SUMMARY What is the future of evolutionary developmental biology? This question and more were discussed at the inaugural meeting for the Pan American Society for Evolutionary Developmental Biology, held August 5–9, 2015, in Berkeley, California, USA. More than 300 participants attended the first meeting of the new society, representing the current diversity of Evo-Devo. Speakers came from throughout the Americas, presenting work using an impressive range of study systems, techniques, and approaches. Current research draws from themes including the role of gene

regulatory networks, plasticity and the role of the environment, novelty, population genetics, and regeneration, using new and emerging techniques as well as traditional tools. Multiple workshops and a discussion session covered subjects both practical and theoretical, providing an opportunity for members to discuss the current challenges and future directions for Evo-Devo. The excitement and discussion generated over the course of the meeting demonstrates the current dynamism of the field, suggesting that the future of Evo-Devo is bright indeed.

EVO-DEVO IS DEAD! LONG LIVE EVO-DEVO!

During the course of my PhD, I have heard several times that evolutionary developmental biology (Evo-Devo) has reached the end of its usefulness. Nevertheless, I and others have continued working in this purportedly dying field. Several recent articles have explored the prospects for evolutionary developmental biology and the role that it plays, or does not, in the broader biological context (Abouheif et al. 2014; Laland et al. 2014; Love 2015; Minelli 2015; Moczek et al. 2015). Regardless of their outlook for the field, the presence of these articles demonstrates that this is a dynamic time for Evo-Devo. The recent formation of a new society: the Pan-American Society for Evolutionary Developmental Biology (evodevopanam.org), and the excitement generated by the 300+ participants at the inaugural meeting confirms that I am not alone in my interest. The first meeting of this new society was held August 5–9, 2015, at the University of California Berkeley Clark Kerr campus in Berkeley, California, USA. The number of participants, the range of studies, and the ongoing discussion within the field of the goals and capabilities of Evo-Devo demonstrate that the field is as dynamic and exciting as ever. Organizers Nipam Patel (UC Berkeley), Chris Lowe (Hopkins Marine Station, Stanford University), Karen Sears (University of Illinois), and Ehab Abouheif (McGill University), made a concerted effort to invite speakers reflecting the current diversity within the field in terms of the science discussed, and in terms of the speakers invited. The one-room format accentuated this diversity, while emphasizing the

importance of the concepts that bring the field together. Here, I will describe some highlights of the work discussed by invited speakers during the meeting, as well as provide a general overview of the discussions that took place.

BIG QUESTIONS: KEYNOTES AND AWARD WINNERS

The opening plenary talks by Sean Carroll (University of Wisconsin-Madison, HHMI) and Neelima Sinha (University of California, Davis) and the closing award talks by Rudy Raff (Indiana University) and Natalie Pabon-Mora (Universidad de Antioquia) illustrate the scope of the field of evolutionary developmental biology. Changes in gene regulatory networks, the repeated deployment of modular networks to produce novel morphologies, the role of environment in producing morphology, comparisons within and across species and beyond, and the variety of systems and techniques used to ask and answer questions about changes in organismal form through time: these themes and more were brought to the forefront in these talks and throughout the meeting.

Best known for his work on elucidating the role of regulatory changes in phenotypic change, Carroll began the meeting discussing gene co-option and the evolution of novelty, detailing the example of wing spot evolution through repeated cooption of *Wingless* in the fruit fly, *Drosophila guttifera* (Werner et al. 2010). Carroll also discussed the role of gene duplication and the role of loss in diversification; that is, does

diversification follow or precede a loss? This is a big question that deserves further study. Complementing Carroll's talk about gene co-option, Sinha presented a wide-ranging talk on the role of developmental modules in patterning the diversity of leaf forms in the tomato, *Solanum*. This group has several wild species with varied leaf morphology, and takes advantage of ongoing agricultural research on the domestic tomato plant. Changing leaf morphology relies on the repeated deployment of common regulatory modules (Ichihashi et al. 2014). Sinha also pointed to the future of Evo-Devo, presenting work illustrating the important role of environment on phenotype. For example, leaf morphology is highly dependent on the local environment, and understanding the specific context of leaf growth is important for understanding leaf shape in laboratory and natural environments (Chitwood et al. 2012, 2014).

Evo-Devo pioneer Raff has influenced many practitioners in the community, including me, through his books, such as "The Shape of Life," and his work on the development and evolution of life history strategies in sea urchins. Raff spoke about hybridization experiments in the sea urchins *Heliocadris erythrogramma* and *Heliocidaris tuberculata*, which differ in the mode of development; *H. erythrogramma* embryos develop directly from large eggs, while *H. tuberculata* embryos develop into feeding larvae from small eggs. Reciprocal crosses of these two species showed that larval features could be restored in the *H. erythrogramma*, producing a novel phenotype indicating control of the ancestral larval form is retained (Raff et al. 1999). Raff continues to be active in exploring early developmental forms, exploring taphonomy of early embryos, linking Evo-Devo to its paleontological roots. The controversial description of small soft-bodied forms in the Doushantou formation in China as embryos (Xiao et al. 1998; Hagadorn et al. 2006), led Raff et al. to investigate the potential for embryos to be preserved, demonstrating this possibility via early protein inactivation, and subsequent replacement of tissues by bacterial films (Raff et al. 2006, 2008).

Effectively demonstrating the dynamism of the young researchers in the field, early career recipient Pabon-Mora presented some of her work on fruit and floral evolution in basal plants. Pabon-Mora's work explores the evolution of fruit and flower morphology by looking outside the standard *Arabidopsis* model. Judiciously choosing species to complement existing models has yielded valuable information about the evolution of fruit development genes in flowering plants (Pabon-Mora et al. 2013, 2014). Pabon-Mora discussed innovative ongoing work, which promises to continue to excite interest.

INVITED SPEAKERS: A SMORGASBORD OF EVO-DEVO

Regulatory changes and gene regulatory networks

One of the major contributions of Evo-Devo to understanding the evolution of form has been understanding the role of

changing connections and components of genetic regulatory networks. Veronica Hinman (Carnegie Mellon University) leverages work on developmental networks in *Strongylocentrotus purpuratus* and related echinoderms, focusing on the role of transcription factors. Although *cis*-regulatory elements in the genome are recognized as important sites for changing network connections, less is understood about the role of transcription factors themselves. They appear to be more important than previously thought, and modularity within transcription factor motifs appears to be a source of variation in gene networks (Cheatle Jarvela and Hinman 2015). Taking advantage of another well-known system for ecology and evolution, Craig Miller (University of California, Berkeley), uses the stickleback, *Gasterosteus aculeatus*, to study cranio-facial evolution. Marine sticklebacks have repeatedly invaded freshwater habitats, subsequently undergoing adaptive radiations. Using genome-wide linkage mapping and quantitative trait loci (QTL), Miller and others identified several loci implicated in various skeletal changes (Miller et al. 2014). Gill raker number and spacing appear to have evolved using similar developmental mechanisms (Glazer et al. 2014), while tooth number appears to increase using divergent developmental mechanisms (Ellis et al. 2015). The increased number of pharyngeal teeth has been linked to *cis*-regulatory changes in *Bmp6*, identified in previous QTL screens (Ellis et al. 2015). These complementary approaches demonstrate the complexity of Evo-Devo, highlighting the need for interdisciplinary techniques.

Environment and plasticity

The role of environmental variation and developmental plasticity in producing morphological variation is increasingly dominant. Presenting a variety of animal and plant examples of asymmetry, Richard Palmer (University of Alberta) highlighted questions regarding the role of environment, genes, and plasticity in producing left-right asymmetries (Palmer 2009). In most cases it appears that environment plays a key role, that is, genes are followers in the origin of asymmetries (Schwander and Leimar 2011). Palmer also highlighted examples of the role environment plays in altering morphology during development, including the role of diet in producing different claw types (Palmer 2012). Rolf Sommer (Max Planck Institute for Developmental Biology, Tuebingen) discussed the role of plasticity in the development of morphological novelties. The nematode, *Pristionchus pacificus*, exhibits an environmentally controlled polymorphism, producing robust teeth under predatory-inducing conditions (Ragsdale et al. 2013). This dimorphism is controlled by a developmental switch, (Ragsdale et al. 2013), although further work is showing that the underlying regulatory pathway is more complex than initially thought. Ongoing work exploring a highly complex polyphenism in a single nematode species promises to be a fascinating case study of the role of plasticity in the development of new structures.

Novelty

A current area of active research in Evo-Devo is to explain the origins of novel characters. Mark Rebeiz (University of Pittsburgh) described the origins of a novel structure in flies, the posterior lobe. Examining in detail the regulatory region of the *Poxn* gene, a key node in the formation of this structure in the *Drosophila melanogaster* subgroup, Rebeiz's group found conservation of the enhancer region. Further, the gene network leading to the development of the posterior lobe is shared, at least in part, with that of the larval spiracle, and both are regulated by upstream Hox signalling factors. The network that produces the larval spiracle appears to have been co-opted to form genital posterior lobe, a novel structure in the adult (Glassford et al. 2015). Julia Bowsher (North Dakota State University) also presented a novel sexual ornament, taking an integrative approach to the evolution of abdominal appendages in sepsid flies. In these dipeterans, these novel abdominal appendages are used by males to court and mate with females. This sexually dimorphic trait is unique to sepsids, and based on morphological, genetic, and developmental data has evolved once, with three subsequent losses and a single regain (Bowsher et al. 2013). Further work is leveraging behavioral and functional analyses of mating to understand how sexual selection has shaped the abdominal appendages, as well as using transcriptomic tools to understand the changes in control of sexual dimorphism between primary and secondary gains of appendages (Melicher et al. 2014). Addressing the origins of sexual dimorphism, James Umen (Donald Danforth Plant Sciences Center) presented work on volvocine algae, which encompass a transition from single cells to multicellularity, as well as from isogamy to anisogamy and oogamy; that is, from same sized sex cells to dimorphic sex cells, sperm, and eggs (Umen 2014). Two species include a range of multicellular and cell specification states; *Chlamydomonas reinhardtii*, a single celled alga with equal sized mating types, and *Volvox carteri*, a multicellular species that produces dimorphic sperm and eggs. The reproductive cell dimorphism in *Volvox* is controlled by a single gene, MID, which in *Chlamydomonas* controls mating type, illustrating that the ancestral control of mating type was co-opted to control differentiation of reproductive cells (Geng et al. 2014). The new role of MID in controlling sexual dimorphism in *Volvox* makes this an exciting model for understanding where sex comes from.

New techniques

New techniques are opening new vistas in Evo-Devo, both in established models and in less traditional systems. For example, the cnidarian *Nematostella vectensis*, has been developed as a model for the basal metazoa (Marlow et al. 2009; Technau and Steele 2011). Matt Gibson (Stowers Institute) showed new tools in use including the characterization of a red fluorescent protein (Ikmi and Gibson 2010), and the development of genome

editing tools, including TALENs and CRISPR/Cas9 (Ikmi et al. 2014) in order to study the formation and control of epithelia. Applying new techniques in novel ways is also revealing surprising insights. For example, Chris Amemiya (Benaroya Research Institute), presented work leveraging the large and increasing number of sequenced genomes available. Rather than taking the standard comparative approach, his group is looking deeper within genomes to explore novel components. This has led to describing chitin in vertebrates, a biomolecule previously described only in fungi and invertebrate organisms. It is endogenously produced and present in developing zebrafish, larval salamanders, and fish scales (Tang et al. 2015). New tools aren't only for animals: Jocelyn Hall (University of Alberta) is working to understand the evolution of floral symmetry in the Cleomaceae, which are sister to the *Arabidopsis*-containing Brassicaceae. Hall is exploring the developmental basis of different developmental patterns leading to a symmetrical flower (Patchell et al. 2011), using virus induced gene silencing (VIGS), a reversible virus induced method of silencing specific genes in plants (Lu et al. 2003), to explore the function of the TCP genes implicated in changes in floral symmetry (Martín-Trillo and Cubas 2010).

Non-molecular approaches

Although the field is currently buzzing with excitement around our increased ability to explore non-traditional model systems using new genetic tools, research using non-genomic tools is providing answers that are just as exciting, and generating many new questions. For example, José Xavier-Neto (Brazilian National Sciences Laboratory) has worked on the role of retinoic acid in development and evolution of the chambered vertebrate heart (Simões-Costa et al. 2005; Xavier-Neto et al. 2015). Here, he presented work on cardiac fossilization, wowing the audience with images of putative intermediate fish hearts to corroborate evolutionary hypotheses (Simões-Costa et al. 2005). Manu Prakash (Stanford University) gave a fascinating talk on the use of *Trichoplax adherens* as a physical model of cell movement in living tissues. Several biological aspects of this enigmatic basal animal group have been described, including cell types (Smith et al. 2014), however, Prakash and his group are taking advantage of their two-dimensional structure to label and track cellular movements in order to model organismal fluid mechanics (Dumont and Prakash 2014). Prakash also demonstrated his Foldscope microscope, a low-cost microscope designed for educational and scientific use (Cybulski et al. 2014). Angela Hay (Max Planck Institute for Plant Breeding Research) presented modeling results, in this case in order to understand mechanisms of explosive dispersal in *Cardamine hirsuta*. This close relative of *Arabidopsis* boasts numerous developmental tools (Hay et al. 2014). Hay is now using morphomechanics to predict how changes in cellular parameters could produce the forces necessary to explosively

disperse seeds, and following up by looking for how cells actually develop.

More traditional genetic and embryological methods continue to reveal interesting results. For example, Matt Rockman (New York University), studies the marine polychaete, *Streblospio benedicti*. Females produce either small eggs that develop indirectly as swimming larvae, or large eggs that use endogenous yolk to develop directly into juvenile worms. Genomic approaches are unwieldy in this species, so Rockman's group uses large-scale crosses of the two developmental types to define the genetic controls that produce these alternative developmental types. Certain developmental features such as egg size and the size of the larval gut are maternally determined, while traits such as length of larval chaetae are zygotically determined (Zakas and Rockman 2014). Similarly, Rachel Collin (Smithsonian Tropical Research Institute) uses embryology and phylogenetics to understand the convergent evolution of an alternative developmental phenotype in the calyptraeid gastropods (slipper limpets). Calyptraeids have a range of developmental types, including adelphophagy, a developmental type in which developing encapsulated embryos ingest their developmentally arrested siblings. Adelphophagy is present in many animal groups, and has evolved multiple times within the calyptraeids (Collin 2004). Ecologically, adelphophagy is thought to increase hatching size in some cases, and has been shown to increase variation in hatching size (Collin and Spangler 2012). The details of adelphophagy vary among the calyptraeids, and recent work is exploring this phenomenon in greater detail in *Crepidula navicella* (Lesoway et al. 2014).

Population genetics/genomics

An exciting direction for Evo-Devo is the push towards looking at evolution of development at the population level. Catherine Linnen (University of Kentucky) uses the pine sawfly (*Neodiprion* spp.), an important agricultural pest, to take an explicitly multi-level approach: from genetic mutation to population in order to understand and predict evolutionary changes. Sawflies are a tractable study organism, with a wealth of existing ecological data. Females lay eggs on the needles of evergreens, and Linnen has shown that changes in host-use can drive speciation (Linnen and Farrell 2010). Ongoing work developing genomic and other tools for use with population genomic, behavioural, and morphological study will be well worth watching for. Bob Reed (Cornell University), described work in heliconius butterflies, another group with a rich ecological and evolutionary literature. Gene mapping, expression, and population genetic data have identified *optix* as the single gene controlling red color patterning (Reed et al. 2011), which is also implicated in the diversification of the group (Martin et al. 2014). Reed also works with buckeye butterflies (*Junonia coenia*), which show a seasonal change in wing coloration, again taking an explicit population genetics approach. Wing color

variation differs across populations, and the degree of plasticity or canalization of wing color appears to be genetically controlled (Daniels et al. 2012). Similarly, Stacey Smith (University of Colorado Boulder) takes a population-level approach to diversity. Using the Iochrominae, members of the tomato family, as a model, Smith is exploring the convergent evolution of floral coloration. Flower coloration is controlled by the anthocyanin pathway, and Smith is exploring the different mechanisms for these changes in nature, showing both *cis*-regulatory and coding sequence changes (Smith et al. 2013; Coburn et al. 2015). The repeated evolution of change in floral color allows questions about the mechanisms of evolution to be addressed (Smith and Baum 2006). These population-level approaches, incorporating natural genetic variation are indeed the future of Evo-Devo.

Regeneration

Regeneration, the re-development of body parts or even of the whole body at the adult stage, has taken an Evo-Devo turn in recent years (Bely and Nyberg 2010; Tiozzo and Copley 2015), and several examples were on display. Mansi Srivastava (Harvard University) presented work on a new model for whole-body regeneration, the three-banded panther worm *Hofstenia miamia*. Srivastava's group has produced a suite of tools for studying the process of regeneration in *H. miamia*, focusing on the molecular mechanisms of body re-organization (Srivastava et al. 2014). Srivastava also presented compelling transcriptomic evidence for placement of the group as sister to the rest of the bilateria, suggesting that acoels are an important comparative system for unravelling the evolution of regeneration in metazoans. Alexa Bely (University of Maryland) is using live 3D imaging techniques in the oligochaete annelid, *Pristina leidy*, to address questions about the role of the proposed regenerative stem cell. The highly dynamic cells observed live appear similar to the neoblasts described from static histological work, and ongoing work is determining the possibility of a shared identity with other similar cells in other animal models of regeneration. Vertebrates are also capable of regenerating body parts, and Igor Schneider (Universidade Federal do Para) shared his work on limb regeneration in lungfish. Again, these animals sit in an interesting phylogenetic position in terms of evolution of the vertebrate limb, and Schneider is using them to assess developmental similarities with other regenerating vertebrates. Interestingly, retinoic acid, which is known to play an important role in limb bud anterior-posterior differentiation, has no effect on limb regeneration in the lungfish, however, there is little A–P differentiation in the limb of a lungfish. Other pathways, which control proximal-distal differentiation, are conserved with other vertebrates. These results suggest that at a cellular level, regeneration shares at least some developmental modules across the vertebrates. The question remains as to how deeply homologous this process is. It is clear, however, that the Evo-

Devo approach is proving fruitful in addressing this long-held question about adult development.

WORKSHOPS: LATIN AMERICA, TECHNIQUES, DIVERSITY, EDUCATION, AND THEORY

Latin American challenges in Evo-Devo

As highlighted by several presenters during the course of the meeting, the bulk of the world's biological diversity can be found in the neotropics. This meeting provided an introduction to the type and quality of work being done in Latin America for those outside, as well as an opportunity for Latin American researchers to meet one another; both are important interactions that will lead to future collaborations. There are plans to develop a hub for Latin American research under the umbrella of the society, which will include increased awareness through regular blog posts. A special issue covering Latin American research is also planned for eventual publication in the Journal for Experimental Zoology B.

New and developing tools for emerging model systems in Evo-Devo

New techniques, including modern bioimaging and light-sheet fluorescence microscopy, RNAi, genome editing with CRISPR/Cas9, and techniques for transient functional analyses are changing the face of developmental biology, and have had an outsized effect on the ability of Evo-Devo to develop new model systems and address new questions. The techniques-focused round table session discussed these topics, and the technical details have been made available on the society website (<http://www.evodevopanam.org/techtools.html>).

Diversity in Evo-Devo and the student-mentor relationship

Diversity in science is a dominant issue, and was definitely at the forefront of this meeting. One of the major messages emerging from discussions was the importance of networking and targeting mentorship to communities that have traditionally lacked representation. The idea of dual identities as a representative of an under-represented group in science and as a scientist in under-represented populations was identified as a powerful point of contact and valuable for increasing diversity in the field. This subject affects all scientists, and the meeting organizers should be applauded for their efforts to bring greater visibility to this issue. I look forward to continued efforts to increase diversity at future meetings.

Evo-Devo education

The dazzling array of organismal diversity on display at the meeting inspired all participants, and can also be leveraged as a

teaching tool in science classrooms of all levels. Particularly in these times of budgetary restraint, creating interest and understanding of the goals and successes of the field are important to communicate to a wider educational community. As a starting point, there was a proposal to collect syllabi for placement in a centralized database as a part of the new society's online presence, in particular, for undergraduate teaching.

Theory in Evo-Devo

Evo-Devo attempts to study processes within deeper processes, which will ultimately require us to go further than static network diagrams. This will require dynamic modeling tools, which are lacking at present. The results of this type of theoretical modeling will not be simple (as one of the discussion leaders, Johannes Jaeger quipped, a general theory of Evo-Devo would not fit on a T-Shirt), but will allow the field to address broader issues, assuming current practitioners are thinking about the more general results of their research programs.

DISCUSSION SESSION: THE FUTURE OF EVO-DEVO

A discussion on the future of Evo-Devo, led by panelists Cassandra Extavour (Harvard University, USA), Johannes Jaeger (KLI Institute, Austria), Lena Hileman (University of Kansas, USA), Federico Brown (Universidade de Sao Paulo, Brazil), Mansi Srivastava (Harvard University, USA), and Abderrahman Khila (Institute of Functional Genomics, France), cited the explosion of new genomic data, the ability to do in-depth work in a growing number of plant and animal models, and the ideal placement of Evo-Devo in dealing with the current data tsunami. The integrative nature of Evo-Devo will be of great benefit for the training of future generations of scientists like me to be able to deal with this wave of information, moreover, the large, non-linear challenges society is facing such as biodiversity loss, climate change, human health, medical, and agricultural challenges.

In spite of the overall optimism for the field, there were a few notes of pessimism. Notably, that for a field approaching 30 years of existence, there is a risk of falling into the trap of using emerging techniques for their own sake, while failing to address more difficult biological questions. This question of what Evo-Devo brings to the field of evolutionary biology preoccupies much of the group, and responses ranged from a complete disregard for the ability of current Evo-Devo to address evolutionary theory to the suggestion that mainstream evolutionary biology is already incorporating many of the ideas that Evo-Devo has produced. The general feeling seems to be that the field is lacking in exploration of standing variation within populations and discussion of the role of fitness to the organism apart from underlying mechanisms. In order for

Evo-Devo to increase conceptual breadth, practitioners will have to pull back from the details of developmental evolution, and to consider where their work fits within a broader evolutionary picture. However, the increasing use of testable hypotheses and ability to make predictions, as well as the openness of the community for discussion of evolutionary theory bodes well. The ongoing discussion of what Evo-Devo can bring to evolution (or to development) is a signal that, at least for the discussion participants, Evo-Devo will continue to take an important place in biology. At the end of the day, the future of Evo-Devo is where those doing the work want to take the field.

CONCLUSIONS

This first meeting of the Pan-American Society for Evolutionary Developmental Biology left me with a better understanding of the current state of the field, specifically thinking about how we can better address larger questions in biology. Most importantly, it left me excited for the new possibilities that exist—new data, new models, new and emerging approaches, and thinking about how to apply these to my own work. I look forward to seeing where the field will be at the next meeting of Evo-Devo Pan Am in 2017. Until then, there will be an opportunity to continue these discussions at the next meeting of the European Society for Evolutionary Developmental Biology in Uppsala, Sweden in 2016.

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