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SYMPOSIUM INTRODUCTION

The Evolution of Arthropod Body Plans: Integrating Phylogeny, Fossils, and Development—An Introduction to the Symposium

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Synopsis The last few years have seen a significant increase in the amount of data we have about the evolution of the arthropod body plan. This has come mainly from three separate sources: a new consensus and improved resolution of arthropod phylogeny, based largely on new phylogenomic analyses; a wealth of new early arthropod fossils from a number of Cambrian localities with excellent preservation, as well as a renewed analysis of some older fossils; and developmental data from a range of model and non-model pan-arthropod species that shed light on the developmental origins and homologies of key arthropod traits. However, there has been relatively little synthesis among these different data sources, and the three communities studying them have little overlap. The symposium "The Evolution of Arthropod Body Plans—Integrating Phylogeny, Fossils and Development" brought together leading researchers in these three disciplines and made a significant contribution to the emerging synthesis of arthropod evolution, which will help advance the field and will be useful for years to come.

Introduction

New fossils, insights from comparative developmental studies and growing phylogenetic resolution have greatly improved our understanding of the evolution of the arthropod body plan. The improved resolution of the phylogeny of arthropods has been based largely on new phylogenomic analyses and the incorporation of data from fossil arthropods. A wealth of new early arthropod fossils has been described from well-preserved Cambrian fossils in China (Chengjiang and Kali biotas) and Australia (Emu Bay Shale), and new fossils have emerged from the Burgess Shale deposits of Canada. Restudy of some older fossils has also revealed new information. Developmental data from a range of model and non-model pan-arthropod species have shed light on the developmental origins and homologies of key arthropod traits. Together these lines of evidence provide increased resolution of the relationships among the phases of arthropod evolution, and the nature of evolutionary transitions. The rapid pace of these developments has increased the importance of synthesis across the phylogenomic, paleontological, and developmental communities.

The symposium "The Evolution of Arthropod Body Plans—Integrating Phylogeny, Fossils and Development" was held at the 2017 SICB meeting in New Orleans to bring together leading researchers in these three disciplines. The aims of the symposium were bringing the communities together, fostering crosstalk among them and working together toward developing an integrated synthesis on arthropod evolution.

The symposium was divided into three sessions, each concentrating on one theme: phylogeny, fossils, and embryos. The symposium included a series of excellent talks, each focusing on a specific question, but all touching on the broader questions of arthropod evolution. Perhaps the best indicator of the success of the approach is the fact that in most cases both the talks and the resulting papers touched on more than one of the main symposium themes. Most of the talks are represented as symposium papers in this volume.

Arthropod phylogeny, fossils, and development

An overview of ecdysozoan relationships was provided by Gonzalo Giribet. The monophyly of Ecdysozoa is now beyond dispute (Giribet and Wheeler 1999; Telford et al. 2008). Ecdysozoa is usually divided into three clades: Panarthropoda, Scalidophora, and Nematoida. Despite many advances in the quantity and resolution of phylogenetic and phylogenomic data, the internal relationships among these clades are still in flux. As Giribet presented it, neither one of these three is as robustly supported as we would like (Giribet and Edgecombe 2017). The monophyly of Panarthropoda (traditionally including arthropods, onychophorans, and tardigrades) has been put into question by the inconsistent position of tardigrades. Even when Panarthropoda is resolved as monophyletic, the position of onychophorans and tardigrades, and the question of which of them is the arthropod sister group, varies among analyses. Resolving the topology of relationships among the panarthropod clades is of course critical to the debate on the evolution of the arthropod body plan. The discovery of a diversity of lobopodian fossils from early Cambrian deposits, and phylogenetic analyses that suggested they were the ancestral nexus for arthropods, tardigrades, and onychophorans, has provided the framework for most discussions for more than a decade. Within this framework, onychophorans and tardigrades are thought to preserve many aspects of the ancestral "lobopodian" body plan (Budd 1996; Budd and Telford 2009; Edgecombe 2010; Edgecombe et al. 2014).

New sources of phylogenetic data could help resolve the phylogenetic uncertainties for Panarthropoda. In her talk, Sarah Tweedt evaluated evidence for a stepwise acquisition of arthropod characters within the lobopodan stem group and found low support. Her paper expands upon the possibility of utilizing developmental data, particularly from the structure of gene regulatory networks (GRNs) as phylogenetic data. Focusing on the evolution of arthropod limbs, Tweedt employed the approach to evolutionary novelty introduced by Günter Wagner (2014) to assess whether the position of a limb or its characteristic morphology is a better foundation for establishing homology (Tweedt 2017). Developmental processes are being progressively unveiled through comparative study of mechanisms and the results have often challenged more traditional approaches to assessing morphological homology. She analyzes fossil and molecular clock evidence to propose that lobopods and arthropods rapidly diverged from a cryptic Ediacaran ancestor. The crux of Tweedt's argument is that developmental identity of a limb is distinct from the information that controls the segmental position of the limb along the anterior–posterior axis of the developing embryo. This argument has important implications both for character coding for phylogenetic analysis and for interpreting a lobopod-arthropod evolutionary transition.

Looking more broadly at the fossil record and its contribution to our understanding of the evolution of arthropod character states, Greg Edgecombe emphasized the importance of the fossil record in helping to reconstruct arthropod phylogeny, in association with molecular data. Edgecombe's talk opened the session of fossils, but connected very strongly to the first session on phylogeny, and he and Giribet collaborated on the opening paper (Giribet and Edgecombe 2017). Clearly, any discussion of the internal relationships within Panarthropoda, and between Panarthropoda and its nearest relatives, must take into account the evidence from the remains of the organisms that lived closest to the time of the split between and within these lineages. In his second contribution to this volume, Edgecombe (2017) focuses on the origin of mandibles in the fossil record. The mandible is the defining feature of one of the two major branches of arthropods—the eponymous Mandibulata. Edgecombe uses the mandible as a specific and detailed example for the use of morphology and fossils in creating phylogenetic trees and in dating them. He links the emerging consensus on monophyly of Mandibulata, with Cambrian fossils that demonstrate a series of morphological transitions within stem group members recovered from Orsten-type deposits. He then uses fossil calibrated time trees to identify when the transitions took place and when crown-group Mandibulata evolved and diverged into its major constituent clades. (After the symposium and submission of manuscripts, an alternative view of the origin of mandibulates, emphasizing the importance distinctive larval niches, was published by Aria and Caron (2017).) Finally, Edgecombe draws on the evo-devo literature, citing recent studies that provide a hint as to the molecular underpinnings of the mandible as a defining trait, bringing together all of the themes of the symposium.

Another aspect of the arthropod body plan that can be analyzed through a synthetic approach was presented by Javier Ortega-Hernández. He talked about the homology of the anterior segments of the arthropod body and the evolution of the anterior appendages. In his work (not published in this volume Ortega-Hernández et al. (2017)) he combines data from the fossil record with comparative morphology of recent panarthropods and with recent results from comparative development biology of these animals. Among other things, he traces the evolution and position of the mouth, and the associated hypostome–labrum complex, in different stem-group arthropods and links this to the development of Onychophora. He homologizes the anterior appendages of various stem- and crown-group fossil arthropods with those of extant groups, using data from comparative neuro-anatomy, gene expression patterns, and positional homology. His work represents a true synthesis of different sources of data to give the most complete analysis to date of the evolution and origin of the panarthropod head.

Staying with fossil arthropods, Melanie Hopkins also applied a developmental approach, focusing on trilobites (Hopkins 2017). The remarkable fossil record of different ontogenetic stages in trilobites makes these the best exemplars for studying development in fossil taxa (Fusco et al. 2004; Hughes et al. 2006). Hopkins started by pointing out the key aspects of trilobite life history and evolutionary history that make them ideal for that purpose. She observed that "segmentation" in trilobites might not be true segmentation, but rather a reflection of the structure of dorsal tergites, which may not correspond exactly to true morphological segments. Most of her talk, and the resulting paper, discussed different modes of development, and how these differences in ontogeny can be seen as drivers or constrainers of trilobite evolution. Her detailed work on trilobite ontogeny has identified a series of morphological modules in the trilobite body plan. Individual modules can follow independent developmental trajectories, providing material for natural selection to easily modify body plans through specific changes in the trajectory of individual modules. This work is an excellent example of using fossil ontogeny to understand morphological evolution, linking developmental time and evolutionary time. The work goes as far as to demonstrate a link between certain life history traits and likelihood of extinction. Hopkins concludes by stating that the main hindrance to understanding the link between trilobite development and evolution is the lack of a robust phylogeny—linking back to the first theme of the symposium and the importance of phylogenies.

Joanna Wolfe followed the same approach of trying to understand the life history of fossil taxa. She tried to probe the ecology of the earliest members of the arthropod stem groups using fossils and dated phylogenies to infer ancestral life history characteristics. Specifically, she focused on trying to reconstruct whether direct development or indirect development with ecological metamorphosis is the plesiomorphic state for crown-group Arthropoda (Wolfe 2017). Her analyses show consistently that metamorphosis evolved earlier than the divergence of Ecdysozoa, and that it is thus shared by all Euarthropoda.

A major event in the evolution of arthropods was terrestrialization—the departure from the ancestral marine environment onto land. This is believed to have happened several times convergently through arthropod evolution. Prashant Sharma focused on the evolution of respiratory structures in different arthropod lineages following independent terrestrialization events (Sharma 2017). Sharma's approach is straightforward evo-devo; an analysis of the expression patterns of homologous genes in different lineages in an attempt to identify homologous structures, and thus reconstruct the evolutionary history of attainment of different aspects of the arthropod body plan. His results show that, contrary to many previously published reports, the various respiratory structures are not all homologous to each other. He also shows that the book lungs are homologous to walking limbs.

Ariel Chipman also takes an evo-devo approach. In his talk, he reviewed the GRNs involved in patterning different aspects of the arthropod body plan (Auman and Chipman 2017). His approach is to try and identify specific GRNs that can be identified as character identity networks, and see how they were first assembled and how they evolve over time within arthropods. His talk and paper focus mostly on networks involved in defining segmentation—one of the central aspects of the arthropod body plan. He points out several networks that are fairly well-conserved and well-understood, for example posterior segmentation, and contrasts them with recently evolved networks, such as the terminal system in *Drosophila* and with networks about which our knowledge is still very vague. A major hindrance here, according to Chipman, is not just lack of data, but the fact that GRNs can change through developmental system drift (True and Haag 2001) and there may be so little remaining similarity that it can be difficult to identify conserved networks.

Combining the evo-devo approach with comparative morphology and the fossil record, Elizabeth Jockusch reviewed data on the development of arthropod limbs, to provide a detailed account of the evolution of the different features of limbs (Jockusch 2017). Arthropodization (the existence of jointed limbs) is the second key aspect of the arthropod body plan. Jockusch traces the transformation from the unsegmented lobe-like limbs of the early lobopods to the jointed appendages of upper stem group arthropods, through the appearance of podomeres and joints, and the genes responsible for defining them. She then follows the gradual specialization of the anterior limbs, and the transformation of the protocerebral appendage to the labrum—providing a link with Ortega-Hernández's talk on the evolution of the arthropod head. These anterior appendages are among the best-studied examples of an evolutionary transition between character identities, and Jockusch demonstrates this using character trees, and plotting how the different identities evolved and shifted over evolutionary time.

Finally, linking back to the broader ecdysozoan picture, and to non-arthropod phyla and their role in understanding arthropod evolution, Frank Smith discussed the homology of body regions in tardigrades. He started by reviewing his previously published results showing that tardigrades have lost an intermediate body region (Smith et al. 2016). In his contribution to this volume he and Bob Goldstein report new results on the structure and homology of the tardigrade brain (Smith et al. 2017). Tardigrades have neuropil like structures in the head cavity that are serially homologous to trunk neuropil. The ventral (sub-esophageal) portion of the brain is an extension of the dorsal portion and not a separate ganglionic structure. Their detailed morphological description forms the basis for a model of the evolution of the panarthropod protocerebrum. They suggest that the anterior ganglion evolved from within an ancient circum–esophageal neuropil, to give rise to the panarthropod protocerebrum.

Conclusion

There has been renewed interest in fundamental questions of arthropod evolution, stemming from the surge of fossil, phylogenetic, and developmental data, as illustrated by the talks and papers in this symposium. As our understanding becomes more detailed, the picture becomes more complex, and it is important to bring together workers from different disciplines at this point in time when the consensus is starting to emerge. This symposium provided an excellent synthesis, with most of the talks already bridging the gaps between the different disciplines. We hope that the papers collected in this volume will provide a body of reference material that will help advance the field and will be useful for years to come.

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