

12-2016

## Editorial overview: Insect phylogenetics: an expanding toolbox to resolve evolutionary questions

Gregory W. Courtney  
*Iowa State University, gwcourt@iastate.edu*

Brian M. Wiegmann  
*North Carolina State University*

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# Editorial overview: Insect phylogenetics: an expanding toolbox to resolve evolutionary questions

## Abstract

It is indeed an exciting time to be an insect systematist! The past decade has seen major breakthroughs in our understanding of the evolutionary relationships of insects, due largely to novel tools for the discovery and analysis of phylogenetically informative characters. Many insights, especially on ancient nodes of the insect evolutionary tree, are a direct result of recent phylogenomic studies [1,2]. New technologies for the discovery of morphological characters provide another valuable source of phylogenetic information, help cross-validate phylogenetic hypotheses based on genomic data, and enhance our understanding of character transformation and adaptation. Additional sources of data (e.g., from studies of fossils and the myriad associations between insects and other organisms) can provide further resolution of important phylogenetic and evolutionary questions. Although the explosion of information from morphological and genomic studies, collection databases, imagebases, geographical records, and other sources has led to some bioinformatics challenges, the field has seen the development novel approaches to overcome many of these issues. Our goal in this issue of Current Opinion in Insect Science is to provide a synoptic overview of cutting-edge tools and methodologies used to address questions relevant to insect phylogenetics.

## Disciplines

Ecology and Evolutionary Biology | Entomology | Genetics

## Comments

This is a manuscript of an article published as Courtney, Gregory W., and Brian M. Wiegmann. "Editorial overview: Insect phylogenetics: an expanding toolbox to resolve evolutionary questions." *Current opinion in insect science* 18 (2016): 93-95. doi: [10.1016/j.cois.2016.11.001](https://doi.org/10.1016/j.cois.2016.11.001). Posted with permission.

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Editorial overview: Insect phylogenetics: An expanding toolbox to resolve evolutionary questions

Editors:

Gregory W. Courtney, Department of Entomology, Iowa State University,  
Ames, IA 50011, USA

Brian M. Wiegmann, Department of Entomology & Plant Pathology, North Carolina  
State University, Raleigh, NC 27695, USA

It is indeed an exciting time to be an insect systematist! The past decade has seen major breakthroughs in our understanding of the evolutionary relationships of insects, due largely to novel tools for the discovery and analysis of phylogenetically informative characters. Many insights, especially on ancient nodes of the insect evolutionary tree, are a direct result of recent phylogenomic studies [1,2]. New technologies for the discovery of morphological characters provide another valuable source of phylogenetic information, help cross-validate phylogenetic hypotheses based on genomic data, and enhance our understanding of character transformation and adaptation. Additional sources of data (e.g., from studies of fossils and the myriad associations between insects and other organisms) can provide further resolution of important phylogenetic and evolutionary questions. Although the explosion of information from morphological and genomic studies, collection databases, imagebases, geographical records, and other sources has led to some bioinformatics challenges, the field has seen the development of novel approaches to overcome many of these issues. Our goal in this issue of *Current Opinion in Insect Science* is to provide a synoptic overview of cutting-edge tools and methodologies used to address questions relevant to insect phylogenetics.

Although many insights on insect phylogeny can be attributed to an expanded array of new molecular tools, the role of morphology and other biological attributes in evolutionary studies has not diminished. Indeed, insect systematics... and systematics in general... is a “cumulative” science that utilizes both traditional and modern data to address contemporary evolutionary questions. Morphological methods such as basic photomicrography, scanning electron microscopy (SEM), and histology remain staples of

the discipline and continue to provide insights into both relationships and character evolution. Wipfler et al. discuss these methods and many novel techniques for discovery of structural characters, including confocal laser scanning microscopy, nuclear magnetic resonance imaging, micro-computed tomography ( $\mu$ CT), computer-based 3D reconstruction, and others. All provide not only a suite of previously unstudied homologies and new insights on character evolution, but important cross-validation and plausibility assessment for molecular phylogenetic studies.

The exponential growth in the size and scope of molecular data sets has revolutionized our understanding of insect phylogeny, particularly some of the most controversial and historically challenging nodes of the tree (e.g., monophyly and relationships of Polyneoptera, phylogenetic placement of Strepsiptera and Hymenoptera). Advances in phylogenomics and bioinformatics has provided powerful new tools such as next generation sequencing, and ambitious projects such as 1KITE (see <http://1kite.org>). Several contributions to this issue (Kjer et al., Yeates et al., Maddison) delve into this arena, discussing various genomic methodologies that permit efficient analyses of large datasets. Next-Gen-enabled molecular systematics has transformed the field by providing ready access to thousands of genetic markers where previously inferences from only one or a few genes obtained by PCR and Sanger sequencing made resolution of major radiations seem nearly intractable [3] (Maddison). Despite major advances in our understanding of insect phylogeny, resolution of some nodes has remained elusive (e.g., higher relationships of Palaeoptera and Acercaria/Paraneoptera).

Historically, molecular data has been available almost exclusively via collection of fresh material and preparation of specimens utilizing special techniques. Unfortunately, this has often precluded analysis of the vast repositories of existing specimens in biological collections. Thanks to recent advances in next-generation sequencing and development of techniques for preparing historical DNA, the use of museum specimens is no longer an insurmountable obstacle. Yeates et al. review tools currently available to incorporate the preserved DNA in museum specimens into modern genetic studies (e.g., hybrid enrichment technologies), and discuss the potential rewards and challenges for utilizing

existing biological collections to gather genetic information. In an era of increasing commitments to collecting, export and import permit application, and reporting (“time tax” *sensu* Maddison), any new technologies that permit analysis of existing collections are welcome.

Use of fossils in phylogenetic reconstruction has long been a contentious issue, partly because of the fragmentary nature of the fossil record but perhaps mostly because of the presumption that fossils can be used only for morphology-based analyses. Ware & Barden review protocols for incorporation of fossils in insect phylogenetic hypotheses based on both “traditional” morphological analyses and combined molecular and morphological analyses. They also present a clear historical trend of increasing use of fossils as terminal lineages and in combined analyses, discuss the growing importance of fossil data in both phylogenetic reconstruction and for node calibration in divergence estimation, and argue that careful fossil calibration will provide insights on both morphological evolution and biogeographical history.

Because of their diversity, abundance, and myriad interactions with other organisms, insects can be ideal models for studies of coadaptation, cospeciation, and cophylogeny. Cruaud & Rasplus review the role of large-scale cophylogenetic studies in identifying patterns of cospeciation involving insects. Phylogenetic data play a critical role in providing the temporal and spatial context for testing hypotheses about how these interactions are assembled and maintained through time and allow a more accurate identification of adaptations and the biological context for explaining the evolution of specialized interactions [4].

The growth of internet-accessible databases, imagebases, interactive keys, and other online resources has made digital tools an integral part of modern insect systematics, especially as projects become increasingly collaborative & global. Dietrich & Dmitriev review progress on digital resources for insect systematics, including tools for real-time data acquisition (e.g., specimen and field data) to efficient methods for capturing legacy data from existing collections. High-throughput digitization methods (e.g., whole drawer

scanning of pinned collections) have the potential to efficiently capture both label data and morphological information on millions of specimens. It follows that these same approaches could revolutionize the capture of phylogenetically informative data. Dietrich & Dmitriev posit further that cybertaxonomic software may ultimately lead to, among other things, automated capture of character data, generation of descriptions, construction of keys, and identification of unknowns. Given the current taxonomic impediment, such tools may be critical to progress in better understanding insect biodiversity across the globe.

The explosion of digital information on insects has had major impacts well beyond the professional systematist. The combination of inexpensive, high-quality digital photography and near universal Internet access has greatly accelerated the “democratization” of information on insect biodiversity [5]. Dunn & Beasley equate this to various citizen science projects involving birds, which take observations and non-destructive samples (e.g., images) that then are used to render species distributions and, in some cases, how those distributions are changing. Large online communities such as BugGuide.net and DiscoverLife.org are at the forefront of such endeavors. For example, BugGuide.net, a site with over one million images posted by over 32,000 contributors (as of October 2016), is not only a valuable resource for information on natural history and distributions (including spread of invasive species), but has enhanced discovery of new species and collaborations between citizen scientists and professional systematists. The latter has often provided important data and specimens for both taxonomic revisions and phylogenetic studies [6]. Dunn and Beasley provide additional examples that demonstrate the value of similar collaborations. The ability to more rapidly and efficiently digitize, manage, and disseminate specimen data is already providing important information on the presence, movement, and distributional range of rare, invasive, or emerging pest species. New workflows using cyber-enabled technologies will also be instrumental in accelerating the description, cataloging, and conservation of insect biodiversity.

Historically, conservation priorities have emphasized ecological or cultural criteria, often targeting areas with exceptional species diversity, pronounced endemism, high levels of

endangerment, and/or the presence of "charismatic" taxa. Approaches based on phylogenetic criteria (e.g., diversity or endemism) have received somewhat less attention, yet hold much promise for conservation management. Using an example from the New Zealand fauna, Buckley highlights the value of phylogenetic information in conservation management of insect species and of ecological communities in general. He argues further that through "conserving genetic or phylogenetic diversity, we are facilitating the ability of lineages to adapt to future environmental changes" Given increasing interest in global climate change and its affect on natural communities, such "phylogenetic" approaches may be warranted. That said, the major challenge to such endeavors include the paucity of information on many resident species and the frequent lack of phylogenetic hypotheses through which to assess lineage diversity. Major increases in the scope of sampling from 'metabarcoding' is already expanding our capacity to monitor and record the vast insect diversity in critical habitats and will provide the specimens needed to track changes in diversity using phylogenetic comparisons of communities [7,8].

As Maddison describes, the genomics revolution has had a profound impact on insect phylogenetics, while at the same time, a strong tradition of authoritative and detail-rich comparative organismal biology remains an irreplaceable cornerstone of the field. Insect systematists have played a leading role in the successful transition to a more fully 'phylocognisant' era in entomology (Maddison), and are rapidly expanding the evidence-base for revealing insect phylogeny, interpreting patterns of diversification, and enabling a more complete, multidisciplinary, and integrated science for revealing, conserving and predicting the dynamic history and influence of insects on our changing planet.

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