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## Phylogeny of Holometabola: state of the art

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The rise and diversification of Holometabola — insects with complete metamorphosis — ranks as one of the most remarkable events in all of evolutionary history. The evolution of holometabolous insects is a story of morphological specialization coupled with explosive speciation, the likes of which remain unparalleled in any other organismal group. Holometabola includes approximately 80% of all described insects and over half the total number of all species on Earth, and these numbers will certainly climb as a plethora of undescribed species are gathered from all over the globe and added to this group on almost a daily basis. The majority of holometabolous insects are placed in the four megadiverse orders: Coleoptera (~500 000 spp.), Diptera (~150 000 spp.), Lepidoptera (~160 000 spp.) and Hymenoptera (~150 000 spp.). The remaining seven orders are considerably less diverse (200–7000 spp. each), yet they include highly specialized forms, such as fleas (Siphonaptera) and twisted-winged parasites (Strepsiptera), or are remnants of what were once more diverse groups (e.g. Raphidioptera and Mecoptera). In every sense of the word, Holometabola is diversity: diversity in life history, diversity in morphology and diversity in species.

While entomologists have long been humbled by the immense size of Holometabola, understanding the patterns of diversification among and within these distinct lineages has largely eluded scientific investigation for well over two centuries. With the exception of the scorpionflies (Mecoptera; see Whiting 2002 herein), each holometabolous insect order is well supported as a monophyletic group, but relationships among most orders are dubious, and in some cases controversial. A child can tell a beetle from a wasp from a butterfly, but even the entomological erudite is left pondering which two insects are more closely related. The same general confusion exists over phylogenetic relationships among major lineages within most holometabolous insect orders; some consensus among workers does indeed exist, but overall there are more questions than answers. This is certainly due in part to the extreme morphological specialization: those unique sets of characteristics which allow a group to radiate, but which wipe away much of the evidence of past ancestry (fleas have no wings!). This is also probably

a logistical result of dealing with the bewildering array of species that one must account for within any reasonable phylogenetic estimate for a major lineage. But, it must also be acknowledged that our limited understanding of higher level insect phylogeny is associated with the manner in which entomological systematics has operated in the last two centuries, and the constraints placed on studying such overwhelming diversity. Entomological systematics has always been a 'bottom-up' science. The nascent entomologist is instructed to begin specialization on a limited group of species, and then slowly, meticulously, to work up through genus and family. The very best and brightest may even matriculate to become a specialist on a single order — certainly an admirable accomplishment given the size of most insect orders — but relatively few entomologists have concentrated their efforts on higher level relationships. Therefore, while this strategy has yielded crucial information on a wide variety of specialized groups, the bottom-up approach is ill suited for producing a broad view of insect phylogeny and evolution.

The advent of molecular systematics in the past decade has brought with it not only a new set of tools with which to infer phylogeny, but also the ability to work in the opposite direction: from the top down. By selecting a few exemplars from a broad range of diverse groups for molecular screening, one can view ordinal level insect phylogeny from a new perspective. Although some distractors claim that this new perspective is unfocused, it must be recognized that insect molecular systematics is just emerging as a science with great potential. The first efforts in higher level insect molecular systematics were relatively primitive by today's standards, and even the grandest analyses presented in this volume will seem inadequate by tomorrow's standards. But, it is clear that molecular systematics has not yet reached its pinnacle of usefulness in insects, and many challenges still remain in its application towards higher level insect phylogeny: the challenge to sample a wide range of taxa to more accurately represent the diversity of species contained in each insect order is not a trivial problem given the size of most insect groups; the challenge to generate a wide array of novel

genetic markers which provide more of a species-tree view and less of a gene-tree view of insect phylogeny; the challenge to overcome the computational limitations of enormous data sets. But, at this point in time, these molecular hypotheses — which hinge so clearly on gene selection, taxon representation, methods of analysis, etc. — have done at least one thing: uproot some traditional notions of insect phylogeny and create renewed interest in the exploration and interpretation of morphological data. For the first time in entomology, we are beginning to see a surge of researchers zeroing in on unravelling higher level relationships among insects, tossing their whole arsenal of tools into the fray, and providing exciting new insights into the most wondrous event in evolution: the diversification of insects.

This special symposium volume brings together current research on higher level relationships within the Holometabola. The value in a volume of this sort is not in establishing the final word in insect phylogeny, but in compiling the most current estimates of insect phylogenetic relationships into a single resource, and highlighting what we think we know, and what mysteries still remain. This volume grew from the symposium, 'The Holometabola: phylogeny and evolution of the most successful terrestrial clade', presented at the XXI International Congress of Entomology, Iguassu Falls, Brazil, in August, 2000. This symposium was organized by myself and two contributors to this volume: Brian Wiegmann and David Yeates. The purpose of this symposium was to bring together researchers focused on higher level relationships within the Holometabola, with an eye towards representing every holometabolous insect order. While the majority of symposium participants contributed to this volume, two were unable to contribute and their participation in the symposium should be noted here. Niels Kristensen (University of Copenhagen, Denmark) spoke on the morphological evidence supporting the phylogeny of the holometabolous insect orders, and much of this information can be found

in his most recent review. David Maddison (University of Arizona, USA) presented data on the phylogeny of the beetle suborder Adephaga, and his analyses will appear elsewhere. One author in this volume (Hans Pohl, Institut fuer Biodiversitaetsforschung, Rostock, Germany) did not attend the symposium, but provided important new data on phylogenetic relationships within Strepsiptera. Since relationships among strepsipteran lineages were not discussed in the symposium, it seemed appropriate to include Pohl's contribution to provide a complete coverage of all holometabolous insect orders in a single volume. Some of the papers in this volume are primarily molecular estimates of phylogeny, others are primarily morphological, but all are dedicated towards deciphering the evolution of Holometabola.

A volume such as this is not capable of capturing the depth and breadth of the ongoing research on higher level insect phylogeny, both within and without the Holometabola. For instance, the reader should refer to Volume 28 of this journal for more detailed coverage of the Hymenoptera. Outside of the Holometabola, I am aware of serious research underway on the higher level phylogeny of non-insect Hexapods, the 'apterygote' orders, Ephemeroptera, Phasmida, Plecoptera, Grylloblattoidea, Dermaptera, Blattoidea, Mantodea, Hemiptera, Psocoptera and Phthiraptera. Research on these groups has already yielded exciting new insights into the evolution of insects, and undoubtedly more are to be revealed. This next decade will see insect molecular data sets approaching 10 000 taxa by dozens of genes to provide a grand view of insect diversity and evolution. This volume is dedicated towards spurring these efforts triumphantly forward.

## References

- Whiting, M. F. (2002). Mecoptera is paraphyletic: multiple genes and phylogeny of Mecoptera and Siphonaptera. *Zoologica Scripta*, 31, 93–104.