

A genus-level supertree of Adephaga (Coleoptera)

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Received 14 October 2005; accepted 17 May 2006

Abstract

A supertree for Adephaga was reconstructed based on 43 independent source trees – including cladograms based on Hennigian and numerical cladistic analyses of morphological and molecular data – and on a backbone taxonomy. To overcome problems associated with both the size of the group and the comparative paucity of available information, our analysis was made at the genus level (requiring synonymizing taxa at different levels across the trees) and used Safe Taxonomic Reduction to remove especially poorly known species. The final supertree contained 401 genera, making it the most comprehensive phylogenetic estimate yet published for the group. Interrelationships among the families are well resolved. Gyrinidae constitute the basal sister group, Haliplidae appear as the sister taxon of Geadephaga + Dytiscoidea, Noteridae are the sister group of the remaining Dytiscoidea, Amphizoidae and Aspitytidae are sister groups, and Hygrobiidae forms a clade with Dytiscidae. Resolution within the species-rich Dytiscidae is generally high, but some relations remain unclear. Trachypachidae are the sister group of Carabidae (including Rhysodidae), in contrast to a proposed sister-group relationship between Trachypachidae and Dytiscoidea. Carabidae are only monophyletic with the inclusion of a non-monophyletic Rhysodidae, but resolution within this megadiverse group is generally low. Non-monophyly of Rhysodidae is extremely unlikely from a morphological point of view, and this group remains the greatest enigma in adephagan systematics. Despite the insights gained, our findings highlight that a combined and coordinated effort of morphologists and molecular systematists is still required to expand the phylogenetic database to enable a solid and comprehensive reconstruction of adephagan phylogeny.

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See also **Supplementary material** in the online edition at [doi:10.1016/j.ode.2006.05.003](https://doi.org/10.1016/j.ode.2006.05.003)

Keywords: Adephaga; Cladistics; Phylogenetic systematics; Safe Taxonomic Reduction; Supertree construction

Introduction

Adephaga is the second largest suborder of Coleoptera and comprises ca. 30,000 species in three terrestrial and eight aquatic or hygropetric families (Meruidae, which was first described by Spangler and Steiner 2005,

is not considered here). Numerous efforts have been undertaken to resolve the phylogeny of this group, and themselves show an evolution in terms of the methods and data used. Older phylogenetic studies, such as Crowson (1960), were not based on Hennigian (Hennig 1950, 1966) or cladistic methods, but rather on intuition (see, for example, Wheeler 1995: “Crowsonian phylogenetics”). A Hennigian approach was used in most studies carried out in the later decades of the last

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century. Some of these studies were very detailed comparative investigations focused on a specific body part (e.g. ovipositor of Hydradephaga, [Burmeister 1976](#); ovipositor of Geadephaga, [Bils 1976](#); prothorax, [Baehr 1979](#)) and with Hennigian character evaluation, but without explicit use of the outgroup comparison method (see [Maddison et al. 1984](#)). A large increase in the number of larval studies started in the 1980s (e.g. [Beutel 1986a, 1992a, 1993](#); [Ruhnau 1986](#); [Arndt 1993](#); [Alarie 1997, 1998](#); [Alarie and Larson 1998](#); [Alarie and Balke 1999](#)), with the first comprehensive cladistic analyses of morphological data being published in the 1990s ([Beutel and Haas 1996](#); [Beutel 1997, 1998](#)). Analyses of DNA sequence data followed shortly thereafter. The first studies were largely or exclusively based on 18S rRNA sequences ([Vogler and Barraclough 1998](#); [Maddison et al. 1999](#); [Shull et al. 2001](#); [Ribera et al. 2002b](#)), but sequences of several genes have been used more recently ([Ribera et al. 2002a](#); [Balke et al. 2005](#)).

The main purpose of constructing supertrees (sensu [Sanderson et al. 1998](#)), like total evidence, is to combine the available phylogenetic information to derive an estimate that is more comprehensive than one based on any single information source. In a supertree context, this information amounts to trees with different but jointly overlapping taxon samples and trees restricted to different subgroups of the more inclusive taxon under consideration.

Although supertrees are appearing increasingly in the literature (see [Bininda-Emonds 2004a](#)), the method remains highly controversial. The key points of contention involve what effects the analysis of tree topologies rather than the data upon which they are based have on the accuracy of the resultant supertree (e.g. due to the loss of information inherent in the former as compared to the latter) and, more generally, whether or not this procedure represents a legitimate method of phylogenetic inference. As important as this debate is, a full summary of it is beyond the scope of the present work. We refer the reader to the relevant literature instead, particularly to the exchange between [Gatesy et al. \(2002, 2004\)](#) and [Bininda-Emonds et al. \(2003\)](#) and [Bininda-Emonds \(2004b\)](#). However, it is worth pointing out that even the staunchest critics of the supertree approach (e.g. [Gatesy and Springer 2004](#)) admit that such a framework will ultimately be necessary to reconstruct the Tree of Life.

What we attempt here is the use of supertree construction to combine presently available adephagan phylogenies to reflect the state-of-the-art of adephagan studies, particularly areas of the adephagan tree that remain poorly resolved due to a lack of consensus and/or of sufficient research effort. We also point out potential methodological and technical problems to supertree construction as highlighted in this study, and present and discuss potential solutions to these problems.

Material and methods

Source data

We compiled trees from manuscripts published or in press by December 2004 that were found using a combination of searches of the available databases (e.g. Web of Science, Zoological Record) as well as from a thorough examination of the relevant literature. To be included, a source tree had to meet the following criteria: (1) relationships of all terminal taxa had to be unambiguously established from a figure or from the text; (2) characters used to build the tree had to be clearly specified; and (3) trees had to contain some novel data and/or be derived from novel analyses with respect to other trees to avoid any pseudoreplication in which a given data set is represented in more than one source tree (see [Gatesy et al. 2002](#)).

As a result, a considerable number of studies (e.g. [Forsyth 1968, 1969, 1972](#); [Hlavac 1975](#); [Kavanaugh 1986](#); [Ruhnau 1986](#); [Deuve 1988, 1994](#); [Jaglarz 1998](#)) were not included here. These works contain valuable data, but the systematic conclusions were not presented in a form suitable for the inclusion in our supertree (there was no clear specification of the characters used, the terminal taxa, the relationships of all groups or of the criteria used for the elaboration of the tree). The nomenclature of all source trees was updated and standardized according to the recent catalogues of [Nilsson \(2001\)](#) and [Löbl and Smetana \(2003\)](#), and completed with other source references where necessary. Because of the large number of species of Adephaga, many of which are poorly studied at best, we used genera as the terminal taxa in this study. In source trees where species formed the terminal taxa and the genus in which they are currently placed was not reconstructed as being monophyletic, either some of the species were considered to belong to a different, 'informal' genus (e.g. "*Stictotarsus* gr.", corresponding to a group of species within the genus *Stictotarsus*; [Ribera 2003](#)), or all relevant taxa were collapsed to a polytomy for that node.

The generally poor overlap between the published phylogenetic trees made it necessary to use a backbone taxonomy (see Appendix A in the online edition at: [doi:10.1016/j.ode.2006.05.003](https://doi.org/10.1016/j.ode.2006.05.003)) as an additional source tree, particularly to guide the placement of those genera with insufficient representation in the source trees. This procedure has been shown in simulation to improve the efficacy and accuracy of supertree construction ([Bininda-Emonds and Sanderson 2001](#)), albeit at the cost of including a source tree that, in this specific case, might not fulfil the above criteria 2 and 3. However, the poorly resolved nature of the seed taxonomy means that it will be easily overruled by any of the other, more robust source trees (in contrast to using the taxonomy as

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