Available online at www.sciencedirect.com

ScienceDirect

Molecular Phylogenetics and Evolution 47 (2008) 783–798

MOLECULAR
PHYLOGENETICS
AND
EVOLUTION

www.elsevier.com/locate/ympev

Towards the phylogeny of chafers (Sericini): Analysis of alignment-variable sequences and the evolution of segment numbers in the antennal club

Dirk Ahrens [a,b,*], Alfried P. Vogler [b,c]

[a] *Zoologische Staatssammlung München, Münchhausenstr. 21, 81247 Munich, Germany*
[b] *Department of Entomology, Natural History Museum, London SW7 5BD, United Kingdom*
[c] *Division of Biology, Faculty of Life Sciences, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, United Kingdom*

Received 17 August 2007; revised 7 February 2008; accepted 8 February 2008
Available online 23 February 2008

Abstract

Scarabaeoid beetles display a distinctive lamellate antenna carrying olfactory sensillae which show various trends of surface enlargement, including the increased number of the terminal lamellate antennomeres. The presence of >3 lamellae ('plurilamellate' antennae) in some groups has been used in the classification of chafers (Melolonthinae) and in particular in the tribe Sericini. However, this character may not be phylogenetically conservative. Here we present a phylogenetic analysis based on partial 28S rRNA, cytochrome oxidase I (*cox1*) and 16S rRNA (*rrnL*) for 183 species of Scarabaeidae, representing all traditionally recognized subfamilies, with particular focus on Sericini. Alignments of length-variable sequences were obtained applying various alignment algorithms and parameter settings. Tree topologies from the combined analysis were very similar when *rrnL* alignment was based on the progressive alignment algorithm MAFFT, MUSCLE, and less so Clustal, but differed greatly when using the probabilistic PRANK and the 'local' alignment procedure BlastAlign, while alignment conditions for the smaller 28S rRNA had little impact on the combined analysis. Preferred conditions were chosen based on an extensive analysis of character congruence between markers and recovery of well established taxonomic groups. Combined analyses on the best alignments using parsimony, maximum likelihood and Bayesian inference generally supported the traditional classification, including the monophyly of Scarabaeidae, with Glaphyridae as its sister, the monophyly of Cetoniinae, and the monophyly of most tribes included. Various levels of support were also obtained in favor of a proposed sister relationship of Sericini with Ablaberini, their close relationships to a melolonthine clade consisting of several tribes with exclusively Southern Hemisphere distribution, and the monophyly of Old World Sericini. In contrast, the generic level relationships were not consistent with the existing taxonomy. The large genera *Neoserica*, *Microserica*, and *Maladera* each split in several distantly related branches. The segment number of the antennal club when optimized onto the preferred tree revealed that plurilamellate antennae originated repeatedly (9–10 times in Sericini, plus multiple origins in other Melolonthinae). This invalidates the use of this trait in the generic classification. The number of lamellae is likely to be relevant to mate recognition, as it affects the spatial organization and number of olfactory sensillae. The high level of homoplasy in antennal characters may indicate a causal link between the morphological diversity of the antennae and the great species richness of Sericini and related melolonthines.

© 2008 Elsevier Inc. All rights reserved.

Keywords: Scarabaeidae; Melolonthinae; Classification; Progressive sequence alignment; Antennal lamellae; Chemical communication; Sexual selection; Species diversification

1. Introduction

The Scarabaeidae Pleurosticti (Erichson, 1847) are a well characterized group of some 25,000 described species of beetles (Scholtz and Grebennikov, 2005) which includes

---

[*] Corresponding author. Address: Zoologische Staatssammlung München, Entomology, Münchhausenstr. 21, 81247 Munich, Germany. Fax: +49 (0)89 8107300.
E-mail address: ahrens.dirk_col@gmx.de (D. Ahrens).

1055-7903/$ - see front matter © 2008 Elsevier Inc. All rights reserved.
doi:10.1016/j.ympev.2008.02.010

more than two thirds of all species in the superfamily Scarabaeoidea (=Lamellicornia). They are defined by a distinct synapomorphy, the placement of the abdominal spiracles on the upper portion of the sternites (e.g. Balthasar, 1963; Ritcher, 1969). The Pleurosticti are usually subdivided into four major subfamilies, including Dynastinae, Rutelinae, Melolonthinae, and Cetoniinae, plus several small groups. All are phytophagous; the adults usually feed on leaves, flowers and pollen, while the larvae feed primarily on living roots, soil humus or decaying wood. The tribe Sericini is a particularly diverse group with some 3500 species in about 200 genera. Like other members of the Melolonthinae, they feed on leaves of angiosperm plants as adults and on roots in the larval stages. They occur predominantly in the Old World, while only five genera are known in the Neotropics (Evans and Smith, 2007) and they are absent entirely from the Australian region. Sericines are inconspicuous and morphologically uniform. Their homogeneity and the resulting taxonomic difficulties have limited studies of their distribution, ecology, and morphology (e.g. Scholtz and Chown, 1995; Ahrens, 2006a).

An important synapomorphy of all scarabaeoid beetles, including the Pleurosticti, is the distinctive lamellate antenna consisting of several leaf-like terminal segments (Browne and Scholtz, 1999). These lamellae are the location of olfactory sensillae (Meinecke, 1975; Leal et al., 1998) required for the detection of feeding sources as well as mate finding and recognition (Reinecke et al., 2006). While most lineages of Scarabaeoidea possess a short antennal club composed of three antennomeres, here referred to as 'trilamellate', a large group of pleurostict scarabs shows various modifications and enlargement of this structure. The two major trends are modification of the common funicular (spherical or cylindrical) antennomeres into lamellate (layered) antennomeres, in particular in the males, and the increased number of lamellate antennomeres from the modal three, to between four and seven. This increased number of lamellae can be referred to as 'plurilamellate', following Burmeister's (1855) German term 'mehrgliedrig' [=with more (than 3) segments]. The number of antennomeres composing the club in the male sex is the most easily recognizable diagnostic feature, and the current classification of Sericini at the genus-level is largely based on these antennal characters. For example, sets of species have been separated into two different genera because the antennal club was composed of three vs. four antennomeres (Reitter, 1896; Brenske, 1897). However, variation in number as well as size and shape of clavicular antennomeres are also seen in other pleurosticts, rendering these traits homoplastic. This fact may raise doubts about the validity of antennal characters as a major trait for the generic classification of Sericini. Yet, the phylogenetic context of antennal traits can not be established conclusively, as relationships within Sericini remain poorly known (Ahrens, 2006a). This also hampers the efforts to examine the evolutionary biology of chemical communication and their effect on species diversification, in particular in how they relate to the diversification of antennal club characters.

Here we address relationships in Sericini using partial sequences from two mitochondrial genes, cytochrome oxidase subunit I (*cox1*) and the large subunit rRNA (*rrnL*), and one nuclear gene, the large subunit rRNA (28S). The latter two markers were highly variable in length, due to the broad taxon sampling that we used to explore relationships of Sericini with other scarab lineages, introducing uncertainty for the phylogenetic analysis. The difference in evolutionary dynamics of mitochondrial and nuclear rRNA genes would suggest differences in sensitivity to the choice of alignment parameters (e.g. Vogler and Pearson, 1996; Terry and Whiting, 2005). Procedures based on the 'progressive' alignment algorithm of Gotoh (1982), as implemented in ClustalX 1.83 (Thompson et al., 1997) remain very popular, despite shortcomings (Gardner et al., 2005). More recent programs are based on a similar principal strategy of progressive incorporation of sequences into the alignment but optimizing these in various ways for the final alignment outputs. These procedures are now available in programs such as MAFFT (Katoh et al., 2002, 2005), MUSCLE (Edgar, 2004a,b) and PRANK (Löytynoja and Goldman, 2005). Clustal settings have also been widely tested and settings optimized for rRNA genes have been suggested (Wilm et al., 2006). This leaves a bewildering range of algorithms and settings to choose from.

Very few studies make use of this range of alignment procedures to test the reliability of a tree. There is little doubt that alignment parameters and choice of methods not only affect the alignment itself, but also the tree topology (Morrison and Ellis, 1997), and regions suffering from the greatest variability in alignment also are those that produce the greatest differences in topologies (Wong et al., 2008). The selection of alignment parameters therefore is probably the most critical step in phylogenetic reconstructions. While the advent of new or improved methods therefore will greatly help in obtaining better tree estimates from alignment-variable sequences, we need to quantify the effect of their application on tree topologies and any bias resulting from the selection of particular methods.

To decide which alignment parameters and procedures are preferable, the criterion of congruence can be applied, based on the notion that an alignment should be an optimal description of homology (i.e. synapomorphy). Testing initial hypotheses of alignment for their congruence with other information, the preferred alignments are those that optimize overall homology, including data from morphological studies or other gene regions (sensitivity analysis of Wheeler, 1995). This principle was implemented here by testing the congruence between the two length-variable regions, *rrnL* and 28S. We also used a method for 'local' alignments based on the BLAST algorithm which rely on the recovery of small segments of sequence recognized among terminals, providing an alternative procedure for homology assignment against which to test the progressive

Download English Version:

https://daneshyari.com/en/article/2835375

Download Persian Version:

https://daneshyari.com/article/2835375

Daneshyari.com