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Phylogeny of the tribe Athetini (Coleoptera: Staphylinidae) inferred from mitochondrial and nuclear sequence data

Hallvard Elven [*], Lutz Bachmann, Vladimir I. Gusarov

Department of Research and Collections, National Centre of Biosystematics, Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, NO-0318 Oslo, Norway

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ABSTRACT

The Athetini are the largest and taxonomically most challenging tribe in the subfamily Aleocharinae. We present the first molecular phylogeny of Athetini. Nucleotide sequences were obtained from three genome regions for 58 athetine and 23 non-athetine species. The sequenced genes are cytochrome oxidase subunits 1 and 2 (2030 bp), tRNA-Leucine 1 and 2 (154 bp), 16S (628 bp, partial sequence), NADH dehydrogenase subunit 1 (54 bp, partial sequence), and the nuclear 18S gene (999 bp, partial sequence). The Athetini were recovered as paraphyletic with respect to Lomechusini and Ecitocharini. Lomechusini were recovered as polyphyletic, with *Myrmedonota* grouping separately from *Pella* and *Drusilla*. The basal topology of Athetini remained largely unresolved but many apical clades were well supported, e.g. *Geostiba* + *Earota*, *Pontomalota* + *Tarphiota*, *Mocyta* + *Atheta* (*Oxypodera*) + *Atheta* (*Mycetota*), *Liogluta* + *Atheta* (*Thinobaena*) + *Atheta* (*Oreostiba*), and *Lyprocorrhe* + *Atheta* (*Datomicra*). The monophyly of *Atheta* was refuted, as several species of *Atheta* formed well supported clades with members of other genera. Additionally, the following groups were rejected: Strigotina (=Acrotonina) and Dimetrotina *sensu* Newton et al. (2000), *Acrotona sensu* Brundin (1952), *Liogluta* series (Yosii and Sawada, 1976), *Atheta* (*Dimetrota*) and *Atheta* (*Alaobia*) *sensu* Smetana (2004).

New tribal placements are proposed for four genera: *Halobrecta* is removed from Athetini and provisionally placed in Oxypodini; *Thendelecrotona* is removed from Athetini and treated as Aleocharinae *incertae sedis*; *Meronera* and *Thamiaraea* are included in the Athetini.

1. Introduction

Staphylinid beetles (Coleoptera: Staphylinidae) represent one of the major radiations within the phylum Arthropoda. The family is believed to have originated in the early Triassic (~240 mya), and was already a diverse group by the mid-Cretaceous (~120 mya) (Grimaldi and Engel, 2005). Today, the family comprises almost 50,000 described species in 31 subfamilies (Thayer, 2005). However, the number of undescribed species is believed to be several times larger (Grimaldi and Engel, 2005). Staphylinids are widespread on all continents except Antarctica and occupy virtually every terrestrial habitat.

Some lineages within the Staphylinidae have proved particularly successful in terms of species number and ecological diversity. The tribe Athetini Casey, 1910 represents one of the family's major radiations. Cases of adaptive radiation are well documented in other groups of organisms, and though the particular causes can be complex (see e.g. Davies et al., 2004 on the rise of the flowering plants), they are often explained as a result of key adaptive innovations, colonization of new territories, or global shifts in either climate or species communities (Gavrilets and Losos, 2009). Adaptive radiations may occur rapidly (see e.g. Kocher, 2005), and the short time span between cladogenetic events may complicate the task of inferring phylogenies.

The Athetini are the largest tribe in the subfamily Aleocharinae Fleming, 1821, and comprises more than 170 genera and thousands of described species worldwide (Newton et al., 2000). The tribe nests within the so-called "higher" Aleocharinae (Ashe, 1994, 2005), a monophyletic group of at least 46 tribes (Ashe, 2007) supported by several morphological characters (Ashe and Newton, 1993; Ashe, 2005, 2007). Athetines exploit most terrestrial habitats, and are particularly abundant in humid microhabitats rich in decomposing organic matter, such as leaf litter, decaying wood, dung, carrion, mushrooms, mammal burrows, and riparian zones. Examples of more unusual habitats include ant nests and fermenting tree sap. Both adults and larvae are usually predators on micro-arthropods and possibly other micro-invertebrates.

While ecologically diverse, the members of Athetini generally show little morphological variation, and the tribe is considered the taxonomically most challenging group within the Aleocharinae (Newton et al., 2000). The classification of Athetini has been

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[*] Corresponding author. Fax: +47 22851837.
E-mail addresses: hallvard.elven@nhm.uio.no (H. Elven), lutz.bachmann@nhm.uio.no (L. Bachmann), vladimir.gusarov@nhm.uio.no (V.I. Gusarov).

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unstable, and several conflicting and competing classifications for the tribe exist (see Yosii and Sawada, 1976; Seevers, 1978; Muona, 1979; Lohse et al., 1990; Newton et al., 2000; Smetana, 2004). An important reason for this conflict is that all classifications of Athetini following the World catalogue of Bernhauer and Scheerpeltz (1926) and Scheerpeltz (1934) have been based on regional faunas, resulting in only partial overlap in the taxon coverage. Another reason is the high level of conflict in the morphological characters themselves. Even the tribe itself is not well characterized, and its monophyly has never been tested in a rigorous phylogenetic analysis. Seevers (1978) considered the so-called "athetine bridge" of the aedeagus (see e.g. Muona, 1987: Fig. 1) a possible diagnostic character of the tribe. However, the "athetine bridge" is present in several other tribes as well, e.g. Lomechusini Fleming, 1821, and may be a synapomorphy for a larger clade.

Athetini were originally introduced as "group *Athetae*" (Casey, 1910), a subtribe of the tribe Myrmedoniini Thomson, 1867 (currently, the valid name for Myrmedoniini is Lomechusini). For some time the athetines were treated as a subtribe within Myrmedoniini (e.g. Fenyes, 1918; Bernhauer and Scheerpeltz, 1926; Scheerpeltz, 1934), which included additional subtribes now recognized as separate tribes or placed in tribes other than Athetini and Lomechusini. Fenyes (1921) appears to be the first to refer to Athetini as a tribe, but he simply used the name as a replacement for Myrmedoniini on the grounds that the genus *Atheta* Thomson, 1858 was larger and more representative for the tribe than *Myrmedonia* Erichson, 1837 (=*Drusilla* Leach, 1819). Eventually, Athetini became accepted as a tribe separate from Lomechusini (Myrmedoniini) (Benick and Lohse, 1974; Seevers, 1978; Newton et al., 2000; Smetana, 2004).

In most classifications, *Atheta* is by far the largest genus in Athetini, but the delimitation of *Atheta* varies substantially between authors. For example, Seevers (1978) recognized only two species of *Atheta* in his North American checklist, stating that the genus comprised "less than a dozen species" worldwide. In contrast, the Catalogue of Palaearctic Coleoptera (Smetana, 2004) lists 843 valid species of *Atheta*. When treated in the broader sense, *Atheta* is usually subdivided in multiple subgenera (the Palaearctic Catalogue lists 47). However, the systematic ranks of these genus-group names tend to vary between authors or sometimes even between papers of the same author (see discussion in Muona, 1995). The overall trend is to raise rank, and many taxa listed as subgenera of *Atheta* in early catalogues are today treated as genera (cf. Bernhauer and Scheerpeltz, 1926 and Smetana, 2004). None of the ranking decisions have been backed by phylogenetic analyses, and while other athetine genera are usually supported by unique morphological characters (e.g. Lohse, 1971; Benick and Lohse, 1974), the genus *Atheta* appears to be defined by a combination of plesiomorphic character states only.

Few phylogenetic analyses involving Athetini have been published, and none of these addressed the phylogeny of Athetini in detail. Steidle and Dettner (1993) investigated the abdominal tergal gland of adult Aleocharinae, and included a phylogenetic analysis of 11 aleocharine tribes using five morphological and four chemical characters. Athetini were represented by eight species belonging to four genera, but phylogenetic relationships within the tribe were not addressed as all athetines were lumped in a single terminal taxon. Athetini formed a trichotomy with Myrmedoniini (=Lomechusini) and Aleocharini Fleming, 1821, with Oxypodini Thomson, 1859 forming a sister group to the three tribes. Ahn and Ashe (2004) used morphological characters of adult beetles to investigate the phylogeny of the tribe Myllaenini Ganglbauer, 1895 and included in their analysis two representatives of Athetini (*Atheta* and *Pontomalota* Casey, 1885). Athetini was not recovered as monophyletic: the clade containing the two athetine genera also included Lomechusini and Oxypodini (both represented by two genera). Ashe (2005) used larval and adult morphology to investigate the basal phylogeny of Aleocharinae and included three representatives of Athetini (*Atheta*, *Geostiba* Thomson, 1858, and *Pontomalota*). He found strong support for a monophyletic "higher" aleocharine clade, excluding four tribes of "basal" Aleocharinae: Gymnusini Heer, 1989, Deinopsini Sharp, 1883, Trichopseniini

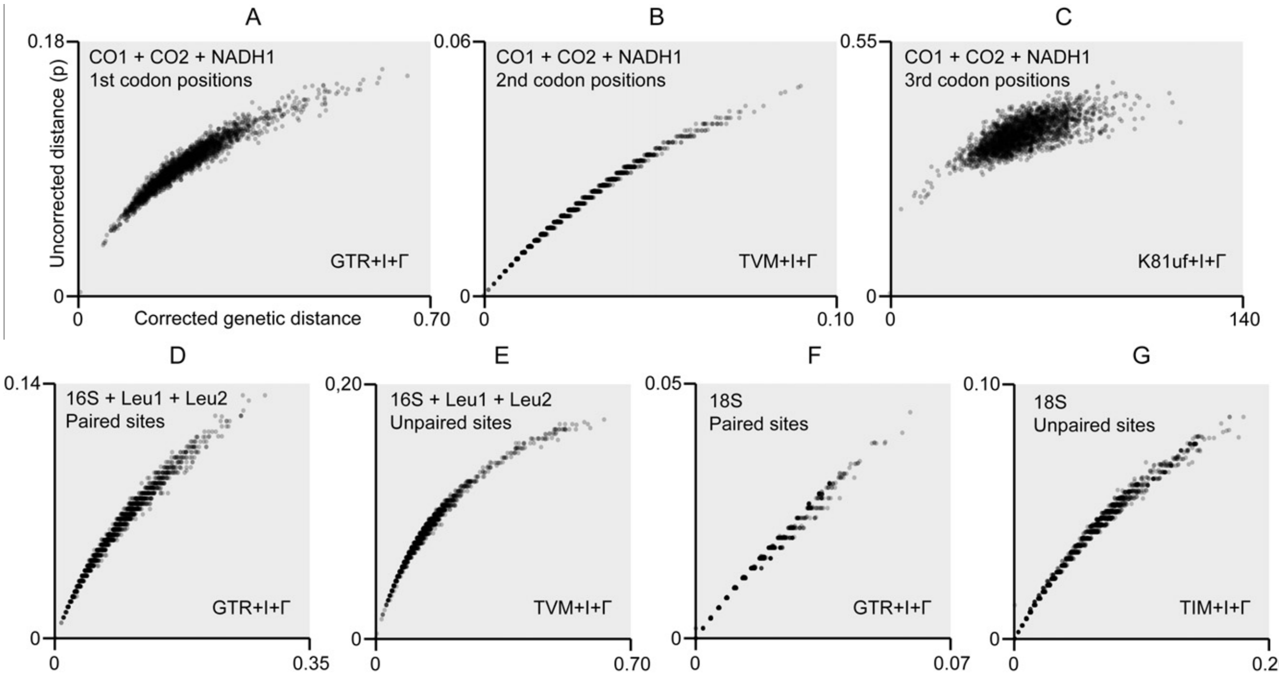

Fig. 1. Saturation plots for seven data partitions. (A–C) Mitochondrial protein coding regions (CO1, CO2, and partial NADH1); (A) 1st codon positions; (B) 2nd codon positions; (C) 3rd codon positions; (D–E) mitochondrial RNA coding regions (Leu1, Leu2, and partial 16S); (D) paired sites; (E) unpaired sites; (F–G) nuclear RNA coding region (partial 18S gene); (F) paired sites; and (G) unpaired sites. The choice of substitution models is based on the Akaike information criterion.