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Cladistic analysis of *Maladera* (*Omaladera*): Implications on taxonomy, evolution and biogeography of the Himalayan species (Coleoptera: Scarabaeidae: Sericini)

Dirk Ahrens

Deutsches Entomologisches Institut im ZALF, Eberswalder Str. 84, D 15374 Müncheberg, Germany

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Abstract

The phylogeny of *Maladera* (subgenus *Omaladera*) is investigated with morphological data. Twenty-one species or subspecies in one of four subgenera of *Maladera* (*Macroserica*, *Maladera*, *Cephaloserica*, and *Omaladera*) were included in the cladistic analysis, with *Stilbolemma sericea* chosen as the outgroup. Data were analysed using two approaches, the parsimony ratchet and heuristic search with successive weighting based on the rescaled consistency index. The results of both analyses provide evidence for the monophyly of the subgenus *M. (Omaladera)* and the group of species occurring in the Himalayas. Each of the three principal lineages of *Omaladera* has diversified independently in separate geographical regions. The present phylogenetic hypothesis provides no evidence that faunal exchange has occurred between these regions as regards ancestral and terminal taxa of *Omaladera*. The phylogenetic analyses support the hypothesis that the strictly parapatric *M. himalayica*, *M. incola*, *M. immunda*, and *M. thakkholae* are valid species rather than subspecies.
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Keywords: Coleoptera; *Maladera*; *Omaladera*; Himalayan clade; Taxonomy; Biogeography

Introduction

Orogenetic processes have influenced climate and evolution in South Asia on a large scale since the breaking up of Gondwana. Due to their extent in width and elevation, the Himalayas have an outstanding position within the tertiary orogenetic belt at the southern margin of the former Cretaceous Asian continent, resulting in an impressive biodiversity which in large parts is still unexplored. Several attempts have been undertaken to investigate the patterns of biodiversity in this mountain chain with the aim of understanding the evolution and origin of its flora and fauna (e.g., Dobremez 1976; Martens 1983, 1993), which in multiple cases have adapted to the harsh environmental conditions at high altitudes. However, proposed conclusions from many of these studies suffer from the fact that modern phylogenetic methods were rarely included.

The taxonomy and distribution of the Himalayan species of the subgenus *Maladera (Omaladera)* (see Appendix A) have been revised (Ahrens 2004). Here, I present a cladistic analysis to shed some light on evolutionary pathways among Himalayan organisms and, in particular, to better understand phylogenetic relations among the Sericini.

E-mail address: ahrens.dirk_col@gmx.de.

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Material and methods

Taxon sampling and characters

Twenty-one species or subspecies in one of four subgenera of *Maladera* Mulsant & Rey – *M.* (*Macroserica*) Medvedev, *M.* (*Maladera*), *M.* (*Cephaloserica*) Brenske, and *M.* (*Omaladera*) Reitter – were included in the cladistic analysis. *Stilbolemma sericea* (Illiger) was chosen as the outgroup due to high probability of group difference in spite of close relations to the ingroup taxa as evidenced by shared apomorphies of "modern" Sericini (Ahrens 2005). Character description and coding was based on 26 species or subspecies belonging to four genera (see Table 1). The material studied for this analysis originated from the following collections: BMNH = The Natural History Museum, London; CA = coll. D. Ahrens, Eberswalde; DEI = Deutsches Entomologisches Institut im ZALF, Müncheberg; MHNG = Muséum d'Histoire naturelle, Genève; MNHN = Muséum national d'Histoire naturelle, Paris; NHMB = Naturhistorisches Museum, Basel; SMTD = Staatliches Museum für Tierkunde, Dresden; TICB = coll. P. Pacholátko, Brno; ZMHB = Zoologisches Museum der Humboldt-Universität, Berlin. The choice of taxa included in the analysis was mainly based on present and historical classifications of the species and subgenera in *Maladera* (e.g., Reitter 1902; Medvedev 1952). Fourty-seven adult characters were scored for this analysis (see also Table 2). The character states are illustrated in Figs. 1–3.

Phylogenetic analysis

The 47 characters (34 binary and 13 multistate) were all unordered and equally weighted. Inapplicable characters were coded as "–", unknown character states as "?" (Strong and Lipscomb 1999). The parsimony analysis was performed in NONA 2.0 (Goloboff 1999) using the parsimony ratchet (Nixon 1999) implemented in NONA, run with WINCLADA vs. 1.00.08 (Nixon 2002) as a shell program. Two hundred iterations were performed (one tree hold per iteration). The number of characters to be sampled for reweighting during the parsimony ratchet was determined to be four. All searches were done under the collapsing option "ambiguous" which collapses every node with a minimum length of zero. State transformations were considered to be apomorphies of a given node only if they were unambiguous (i.e., without arbitrary selection of

Table 1. List of species studied

Species	Distribution	Material deposited at
Maladera cardoni (Brenske, 1896)[a]	Northern India, Afghanistan	CA
M. cariniceps (Moser, 1915)	Korea, SE China	ZMHB, CA
M. dierli (Frey, 1969)	The Himalayas	ZSM, CA
M. emmrichi Ahrens, 2004	The Himalayas	SMTD, CA
M. gardneri Ahrens, 2004	The Himalayas	BMNH, CA
M. himalayica himalayica (Brenske, 1896)	The Himalayas	CA
M. himalayica immunda Ahrens, 2004	The Himalayas	SMTD, CA
M. himalayica incola Ahrens, 2004	The Himalayas	SMTD, CA
M. himalayica thakkholae Ahrens, 2004	The Himalayas	CA
M. himalayica thimphuensis Ahrens, 2004	The Himalayas	NHMB, CA
M. holosericea (Scopoli, 1772)	Europe, Siberia	CA
M. insanabilis (Brenske, 1894)	Arabia to northern Indian subcontinent	CA
M. joachimi Ahrens, 2004	The Himalayas	SMTD, CA
M. lignicolor (Fairmaire, 1887)	China	MNHN, CA, MHNG
M. orientalis (Motschulsky, 1857)	Eastern Siberia, Japan	CA
M. prabangana (Brenske, 1899)	Laos	TICB
M. renardi (Ballion, 1870)[a]	Eastern Siberia, Japan	CA
M. simlana (Brenske, 1898)	The Himalayas	CA
M. spectabilis (Brenske, 1898)	Yunnan, northern Indochina	CA
M. sprecherae Ahrens, 2004	Bhutan	NHMB, CA
M. stevensi Ahrens, 2004	Sikkim	BMNH, CA
M. taurica Petrovitz, 1969	Turkey	CA
M. yasutoshii Nomura, 1974	Taiwan	CA
Nipponoserica koltzei Reitter, 1897[a]	Manchuria, Korea	CA
Pleophylla spec.[a]	Southern Africa	CA
Stilbolemma sericea (Illiger, 1802)	USA	CA

For collection abbreviations, see text under Material and methods.
[a]Not included in cladistic analysis.

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