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## 6 Summary

1) To determine the phylogenetic position of the Sericini (Coleoptera: Scarabaeidae), cladistic analyses were performed. The taxa included in the analysis represent most the “traditional” subfamilies of coprophagous and phytophagous Scarabaeidae, with emphasis on the Sericini and melolonthine lineages. Several poorly studied exoskeletal features have been examined including the elytral base, posterior wing venation, mouth parts, endosternites, coxal articulation, and genitalia. The results of the analysis strongly support the monophyly of the ‘orphnine group’ + ‘melolonthine group’. This clade was identified as the sister group to the ‘aphodiine line’ including *Aphodius* + *Copris*. The ‘melolonthine group’ is comprised in the strict consensus tree by two major clades, with the included taxa of Euchirinae, Rutelinae, and Dynastinae nested together in one of the clades (‘melolonthine group I’). Melolonthini, Cetoniinae, and Rutelinae are strongly supported as being monophyletic, while Melolonthinae and Pachydemini appear as paraphyletic. Sericini + Ablaberini were identified in the analysis to be sister taxa nested within the ‘melolonthine group II’ clade. As this clade is distributed primarily in the southern continents, one could assume that Sericini + Ablaberini are derived from one of these southern lineages. It is plausible that the ancestors of Sericini + Ablaberini and *Athlia* were separated by a vicariance event, such as the separation of the African plate from the rest of Gondwana, while Sericini and Ablaberini likely diversified during early Tertiary, with dispersal of some basal Sericini to South America.

2) The Sericini constitute a monophyletic group based on the following apomorphies: (1) vestigial (9th) sternite in the spiculum gastrale absent; (2) cranial process of the spiculum gastrale filiform, very slender and circular in cross section; (3) glandulae accessoriae with left and right glandulae (1+2) having a common duct to the vagina; (4) basal ostium of phallobase small; and (5) metacoxa enlarged.

3) To explore the diversification patterns of Sericini in the Himalaya, eight monophyletic groups have been analysed using cladistics, including *Anomalophylla*, *Calloserica*, *Lasioserica/Amiserica*, *Maladera* (subgenus *Omaladera*), *Maladera* (subgenus *Cycloserica*), *Serica*, *Sericania*, and *Xenoserica* gen. n./ *Nipponoserica*. The Himalayan region has been treated as unit embracing the complex system of nearly parallel mountain ranges, from North Burma in the east to nearly Afghanistan in the west (approximately between 72° and 91° E and 27° and 36°N).

4) All Himalayan sericine taxa belong to a distal sericine lineage (‘modern’ Sericini), sharing the following apomorphic characters states: the presence of a carina from the cranio-lateral margin of the mesosternum to the mesofurcal arm and the acutely bent anterior anal vein (AA).

5) The phylogenies found show a congruent pattern in groups with similar vertical and/or horizontal distribution. Patterns of vertical and/or horizontal distribution are shown to be of crucial importance for gene flow, dispersal capacity, and for the opportunity to occupy new habitats. In lower montane species, major distal clades are generally restricted to the Himalaya, as revealed in *Omaladera* or *Lasioserica*. Among the montane lineages, the following general pattern of diversification have been hypothesized:

(A) Himalayan xerophilous forms, such as *Sericania*, are supposed to have evolved also in the northern and drier parts of Tibet; this corridor should have been responsible for their interference with areas of north-eastern Asia. With progressing uplift and aridization of northern Tibet, and strengthened monsoon, the basal lineages of *Sericania* have been separated into a North-West Himalayan and East Asian clade.

(B) Multiple events of radiation in Himalayan Sericini along southern slope of Himalaya regarding taxa of the more humid areas of the Himalayan southern slope, such as in *Calloserica*, *Omaladera*, or *Lasioserica*. This hypothesis is mainly supported by the congruent cumulative ranges of certain distal clades of species. The fact, that a great

number of diverse sericine groups performed a strong diversification within these mountain chains, lead to assume that the presence of mountain ranges with the characteristics similar to the present Himalaya predate those diversification processes. Similar patterns result from preliminary cladistic analyses of *Microserica*, *Nepaloserica*, and *Oxyserica*.

(C) Major distal clades of middle to upper montane species show a stronger interference with the mountain regions of eastern Tibet as apparent from cladistic analysis of *Serica*. This would implicate that flight-active organisms of medium and upper montane belt had in present and/or past better opportunities for dispersal along and across higher mountain chains as encountered in the Himalaya or eastern Tibet.

(D) Diversification at eastern margin of Tibetan Highland, with (rather recent) range extension north-easterly and westerly (*Anomalophylla*).

(E) Most of the forms occurring in lowland and in the colline regions of the Himalaya represent taxa with extensive ranges having here a limit of their distribution. To these belong the taxa with range belonging for example to Himalayan-Indochinese or to Himalayan-Indian chorotype. Among the forms of the lowland areas, only a very few developed monophyletic Himalayan lineages, such as the taxa belonging to the *Maladera* (subgenus *Cycloserica*). For this group results of cladistic analysis reveal a separating effect of the Himalayan-Alpine belt. It is postulated that two *Cycloserica* lineages existed before they dispersed into the two separated areas, the northern Indian subcontinent (Himalaya) and the Middle Asian lowland.

6) The occurrence of numerous basal lineages in the Himalaya, additionally, lead to assume that the Himalaya was in historical framework also a "refugium, being able to buffer fluctuations of climate by "orobiom-shifting". These 'refugia' might be related also to special topographical structures such as large river valleys which were able to cross the Great Himalayan chain, as apparent in case of *Xenosericca*. In the Himalaya presently very restrictedly occurring basal lineages of e. g. *Lasiosericca* or *Serica* should be interpreted as relics of former widely distributed clades. The taxa of these clades became extinct in great part, probably also in consequence of competition of the strongly radiating younger lineages.

7) There is comparatively high evidence from range positions of closely related species for allopatric geographical speciation in *Lasiosericca* with the majority of closely related Central Himalayan species occurring allopatrically or parapatrically. However, in the more easterly distributed lineages, this pattern is altered by the contrary, with a great portion of closely related species occurring sympatrically. This differentiated pattern might be attributed to the climatic gradient in present and past which has been characterizing this mountain range at least since onset of monsoon climate with its humid south-eastern summer winds.

8) About 60 % of the Himalayan fauna is composed by locally endemic species. Comparative biogeographical analyses (species similarity, parsimony analysis of endemism) and species' phylogeny reveal evidence to hypothesize two principal centres of endemism in the Himalaya: a north-western centre and a south-eastern centre.

9) Beside numerous newly discovered species, the cladistic analyses result in the following preliminary taxonomic conclusions: *Cycloserica* Reitter, 1896 (= *Leucoserica* Reitter, 1896 syn. n.); *Maladera* (*Cycloserica*) *arenicola* (Solsky, 1876) comb. n.; *Nipponoserica* Nomura, 1972 (= *Pseudosericania* Kobayashi, 1980 syn. n.), *Amiserica antennalis* (Nomura, 1974) comb. n., *Xenosericca* gen. n., *Xenosericca sindhensis* (Ahrens, 2000) comb. n., *X. pindarensis* (Ahrens, 2000) comb. n.

## 7 Zusammenfassung

1) Um die phylogenetische Stellung der Sericini (Coleoptera: Scarabaeidae) zu bestimmen, wurden kladistische Analysen durchgeführt, wobei Taxa der meisten “traditionellen” Unterfamilien koprophager und phytophager Scarabaeidae eingeschlossen wurden. Dabei wurde besonderes Augenmerk auf die Sericini und die maikäferartigen Entwicklungslinien gelegt. Verschiedene bislang wenig studierte Merkmale des Exoskeletts wurden dafür vergleichend untersucht, so zum Beispiel die Basis der Elytren, das Hinterflügelgeäder, die Mundwerkzeuge, die Endosternite, die Hüftgelenke und die ektodermalen Genitalorgane. Die Ergebnisse der Analyse unterstützen stark die Monophylie der ‘Orphninen-Gruppe’ + der ‘Melolonthinen-Gruppe’. Dieser Zweig wurde als Schwestergruppe der ‘Aphodiinen-Linie’ identifiziert, welche hier *Aphodius* + *Copris* einschließt. Die ‘Melolonthinen-Gruppe’ besteht aus zwei wesentlichen Zweigen, unter Einschluss der Euchirinae, Rutelinae und Dynastinae, die zusammen in einem der Zweige vereint sind (‘Melolonthinen-Gruppe I’). Melolonthini, Cetoniinae und Rutelinae sind monophyletisch, während die Melolonthinae und Pachydemini paraphyletisch erscheinen. Sericini + Ablaberini wurden als Schwestertaxa in der Analyse identifiziert, gemeinsam innerhalb des Zweiges der ‘Melolonthinen-Gruppe II’ positioniert. Da Taxa dieses Zweiges sind hauptsächlich in der Südhemisphäre verbreitet, könnte man annehmen, dass die Sericini + Ablaberini von einer dieser südlichen Linien abgeleitet sind. Es wäre plausibel, dass die Stammart von Sericini + Ablaberini und *Athlia* durch einen Vikarianz-Ereignis getrennt wurden, wie zum Beispiel die Trennung der afrikanischen Platte vom Rest von Gondwana. Sericini und Ablaberini haben wahrscheinlich dann während des frühen Tertiärs eine starke evolutive Entwicklung vollzogen, mit der Ausbreitung von Taxa mindestens einer basaler Linie der Sericini nach Südamerika.

2) Die Sericini stellen eine monophyletische Gruppe dar, die sich auf folgenden Apomorphien begründet: (1) vestigiales (9.) Sternit beim Spiculum gastrale fehlt; (2) kranialer Fortsatz des Spiculum gastrale fadenförmig, sehr dünn und rundlich im Querschnitt; (3) Glandulae accessoriae münden in einem gemeinsamen Kanal und Porus zur Vagina; (4) basales Ostium der Phallobasis klein; und (5) Metacoxa vergrößert.

3) Um die Muster der Diversifikation der Sericini im Himalaya zu ergründen, wurden acht hypothetische monophyletische Gruppen mittels kladistischer Analyse untersucht: *Anomalophylla*, *Calloserica*, *Lasioserica/Amiserica*, *Maladera* (subgenus *Omaladera*), *Maladera* (subgenus *Cycloserica*), *Serica*, *Sericania* und *Xenoserica* gen. n./ *Nipponoserica*. Das Himalaya-Gebiet wird als geographische Einheit behandelt, die ein System paralleler Gebirgsketten umfasst und sich von Nord Burma im Osten fast nach Afghanistan im Westen erstreckt (etwa zwischen 72° und 91° O und 27° und 36°N).

4) Alle Sericini des Himalaya können einer distalen Entwicklungslinie (‘moderne’ Sericini) zugeordnet werden, die die folgenden abgeleiteten Merkmalszustände gemeinsam haben: craniolateraler Rand des Mesosternum mit einer Leiste zum Arm der Mesofurca und die anteriore Analader (AA) der Ala spitz geknickt.

5) Die gefundenen phylogenetischen Hypothesen zeigen bei Gruppen mit ähnlicher vertikaler und horizontaler Verbreitung kongruente Muster. Es konnte gezeigt werden, dass die vertikale und horizontale Verbreitung von elementarer Bedeutung für den Genfluss, Ausbreitungskapazität und die Möglichkeit der Besetzung neuer Habitate/ Gebiete sind. Bei Taxa der niedrigen montanen Stufe größere distale Zweige sind auf den Himalaya beschränkt, (z. B. bei *Omaladera* oder *Lasioserica*). Unter den montanen Entwicklungslinien können die Diversifikationsmuster wie folgt allgemein charakterisiert werden:

(A) Diversifikation xerophiler Formen in den Steppenwäldern des Nordwest-Himalaya (*Sericania*), mit wahrscheinlichem Kontakt zu den Ostasiatischen Linien über das nördliche Tibet, welcher mit der weiteren Erhebung und Aridisierung sowie die Verstärkung des Monsuns unterbrochen wurde.

(B) Multiple Radiationsereignisse der Himalaya-Sericini am Südabhang des Himalaya unter den Taxa der feuchteren Gebiete des Himalaya, so zum Beispiel bei *Calloserica*,

*Omaladera* oder *Lasioserica*, was durch kongruente kumulative Areale der distaler Zweige der Arten unterstützt wird. Die Tatsache, dass eine große Zahl diverser Gruppen von Sericinen eine starke Diversifikation am Südabhang vollzogen haben, führt zu der Annahme, dass die Präsenz von Bergketten mit ähnlichen Eigenschaften, wie sie gegenwärtig am Himalaya-Südabhang angetroffen werden, Ausgangspunkt der Radiationsprozesse sind. Ähnliche Muster bei der Diversifikation resultieren aus den vorläufigen kladistischen Analysen von *Microserica*, *Nepaloserica* und *Oxyserica*.

(C) Wie aus der Phylogenie der *Serica*-Arten ersichtlich wird, zeigen größere distale Zweige dieser Arten der mittleren und oberen montanen Stufe eine stärkere Beziehung mit den Bergregionen des östlichen Tibets. Das würde bedeuten, dass flugfähige Organismen der mittleren und oberen montanen Stufe in der Gegenwart und/oder der Vergangenheit bessere Möglichkeiten zur Ausbreitung entlang und über die hohen Bergketten des Himalaya oder des östlichen Tibets hatten.

(D) Diversifikation am östlichen Rand des Tibetischen Hochlands, mit (relativ rezenter) Arealerweiterung nach Nordosten und Westen entlang des Tsang Po (*Anomalophylla*).

(E) Die meisten Arten des Tieflandes und der kollinen Stufe des Himalaya sind Taxa mit ausgedehnten Arealen, die hier ihre Verbreitungsgrenze besitzen. Dazu gehören Arten des Himalayanisch - Indochinesischen oder des Himalayanisch - Indischen Chorotypes. Unter diesen Formen haben nur wenige monophyletische Linien im Himalaya ausgebildet, wie z. B. die Taxa von *Maladera* (subgenus *Cycloserica*). Für sie weisen die Ergebnisse der kladistischen Analyse auf einen separierenden Effekt des tertiären Alpin-Himalayanischen Orogens hin. Es wird postuliert, dass zwei *Cycloserica* existierten, bevor sie sich in die beiden getrennten Gebiete, den nördlichen indischen Subkontinent (Himalaya) und das Tiefland von Mittelasien, ausbreiteten.

6) Das Vorkommen zahlreicher basal Linien im Himalaya darüber hinaus führen zu der Annahme, dass der Himalaya in den vergangenen geologischen Epochen auch als "Refugium" fungierte, indem klimatische Fluktuationen durch eine vertikale / und möglicherweise auch horizontale) Umverteilung der Orobiome zu puffern vermochte. Diese 'Refugien' können zu bestimmen topographischen Strukturen in besonderer Beziehung, wie zum Beispiel großen Durchbruchstätern, stehen, wie anhand der Analyse von *Xenosericca* gezeigt werden konnte. Gegenwärtig in ihrer Verbreitung stark begrenzte Vorkommen basaler Taxa (*Lasioserica*, *Serica*) können als Relikte einer einst weiteren Verbreitung interpretiert werden. Die Taxa dieser basalen Linien sind vermutlich zum großen Teil in Folge der Konkurrenz durch die stark radiierenden jüngeren Linien verdrängt worden.

7) Aus der Lage der gegenwärtigen Areale eng verwandter Arten im zentralen Himalaya kann mit hoher Wahrscheinlichkeit auf allopatrischen Speziation geschlossen werden. Bei weiter östlich verbreiteten Arten ist dieses Muster weniger deutlich ausgeprägt, wo ein großer Teil der nah verwandten Arten sympatrisch vorkommen. Diese beiden alternativen Hypothesen werden mit einiger Sicherheit durch den klimatischen Gradienten im Himalaya von Ost nach West bedingt, der die Region mindestens seit dem Einsetzen des Monsunklimas prägt.

8) Etwa 60 % der Fauna des Himalaya besteht aus lokalen Endemiten. Vergleichende biogeographische Untersuchungen (Artenidentität, Parsimonie Analyse des Endemismus) und die Phylogenie der Arten sind die Basis zur Annahme von zwei Endemismus-Zentren im Himalaya: ein nordwestliches und ein südöstliches Zentrum.

9) Neben zahlreichen neu entdeckten Arten, resultieren aus den phylogenetischen Untersuchungen folgende vorläufige taxonomische Schlussfolgerungen: *Cycloserica* Reitter, 1896 (= *Leucoserica* Reitter, 1896 syn. n.); *Maladera* (*Cycloserica*) *arenicola* (Solsky, 1876) comb. n.; *Nipponoserica* Nomura, 1972 (= *Pseudosericania* Kobayashi, 1980 syn. n.), *Amiserica antennalis* (Nomura, 1974) comb. n., *Xenosericca* gen. n., *Xenosericca sindhensis* (Ahrens, 2000) comb. n., *X. pindarensis* (Ahrens, 2000) comb. n.

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