

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

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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. thakkkholae* 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 under-

standing 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.

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

For collection abbreviations, see text under Material and methods.

^aNot included in cladistic analysis.

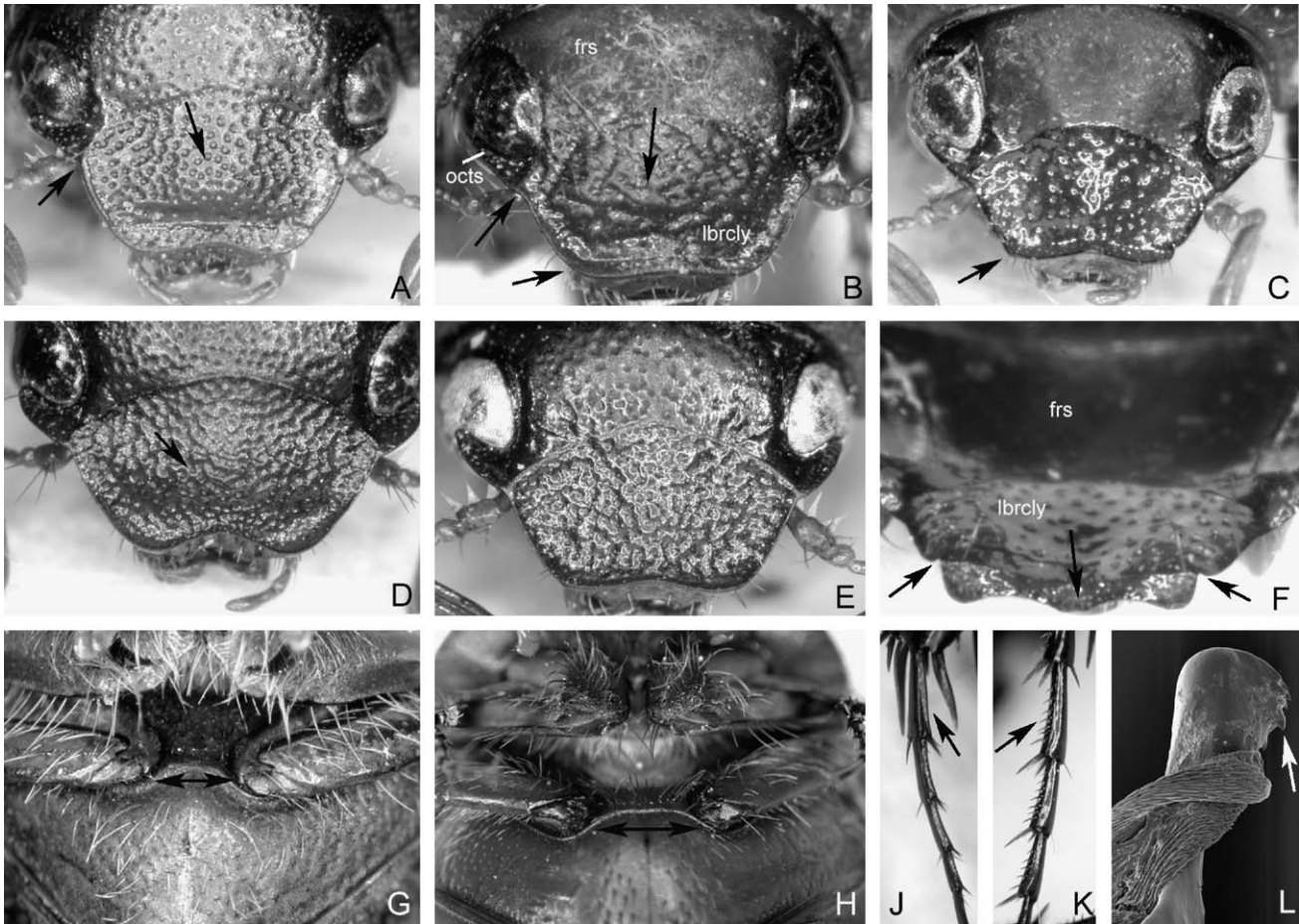


Fig. 1. (A) *Stilbolemma sericea*; (B) *Maladera himalayica*; (C, F) *M. dierli*; (D) *M. taurica*; (E, G, K) *M. holosericea*; (H, J) *M. insanabilis*; (L) *M. simlana*, apex of right paramere. (A–E) head, dorsal view; (F) head, caudodorsal view; (G, H) width of meso- and metasternum between the mesocoxae; (J, K) metatarsomeres, ventral view (not to scale).

accelerated or delayed optimization) and if they were shared by all dichotomized most parsimonious trees. Bremer support (Bremer 1988, 1994) and parsimony jackknife percentages (Farris et al. 1996) were evaluated using NONA. The search was set to a Bremer support level of 12 (based on the number of unambiguous character changes for each node given by WINCLADA), with seven runs (each holding a number of trees from 100 to 500 times multiple of suboptimal tree length augmentation) and a total hold of 8000 trees. The jackknife values were calculated using 100 replications and a 100 search steps (mult*N) having one starting tree per replication (random seed 0). Character changes were mapped on the consensus tree using WINCLADA.

A second analysis was performed with PAUP 3.1.1. (Swofford 1993), running a heuristic search performing TBR branch-swapping (MULPARS option in effect) with branches having maximum length zero collapsed to polytomies. Successive weighting (Farris 1969) was used to further evaluate phylogenetic relationships. This method uses post hoc character weighting based on the fit of each character as applied to the trees currently

in memory. Thus, the “quality” of the character data is used rather than intuitive feeling regarding weighting of characters. Although this method increases the assumptions in the analysis (Siebert 1992), it is useful for analysing phylogenetic pattern when characters exhibit a high level of homoplasy. Characters were reweighted based on the rescaled consistency (rc) index. The maximum value “best fit” option was used, the base weight was set at 100, and indices were truncated. Tree searches continued until the character weights no longer changed (Farris 1988) or until identical trees were found in consecutive searches (indicating stability in the trees).

Characters and character states

In describing character states, I refrain from formulating any hypotheses about their transformation. In particular, coding does not imply whether a state is derived or ancestral. The data matrix is presented in Appendix B.

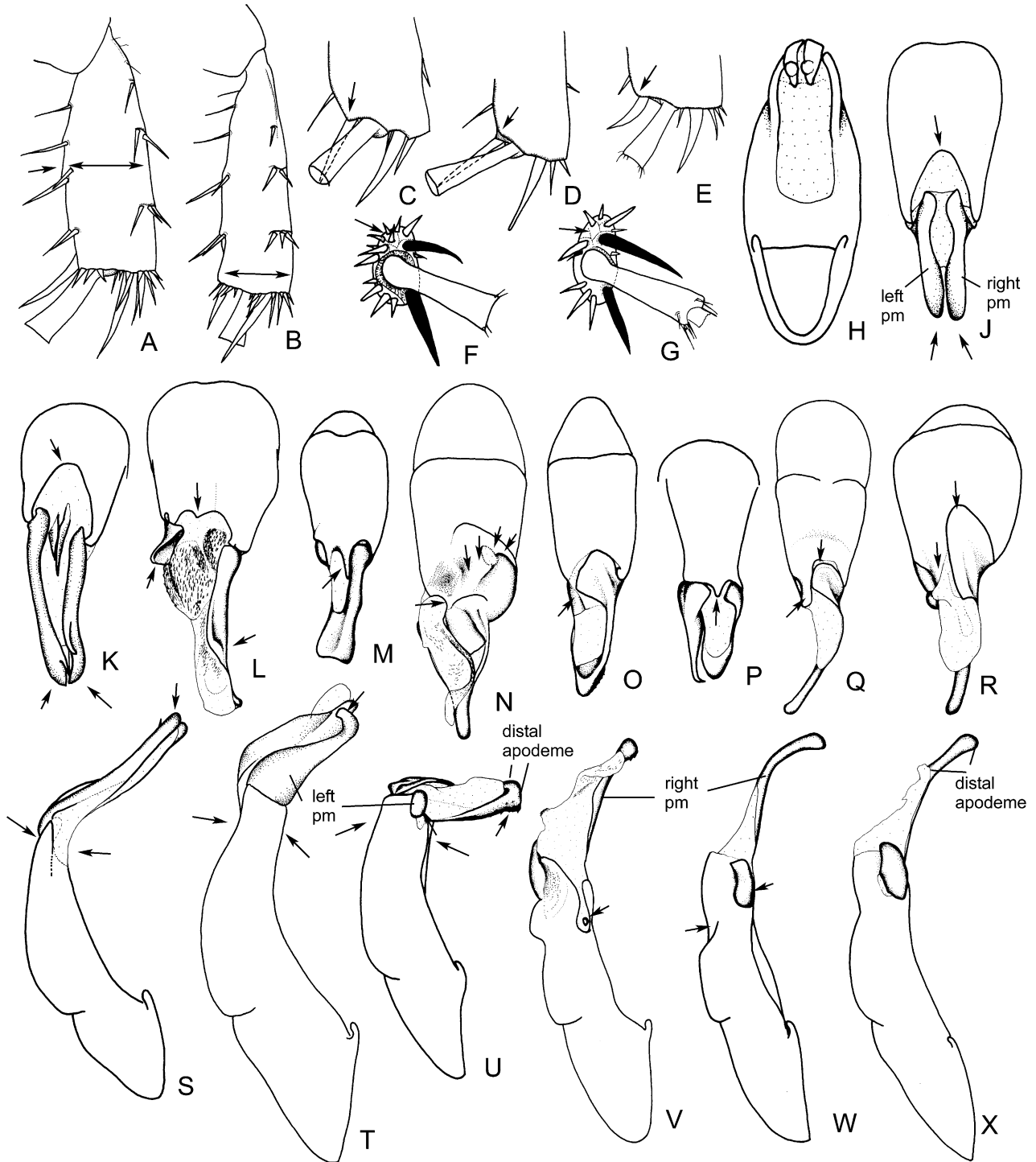


Fig. 2. (A, C, T) *Maladera spectabilis*; (B, D, R) *M. himalayica*; (E) *M. insanabilis*; (F) *M. renardi*; (G) *Pleophylla* sp.; (H) *Nipponoserica koltzei*; (J) *Stilbolemma sericea*; (K, S) *Maladera holosericea*; (L) *M. stevensi*, (M) *M. gardneri*; (N, V) *M. simlana*; (O) *M. dierli*; (P) *M. cardoni*; (Q, W) *M. thakkholae*; (U) *M. sprecheriae*, (X) *M. immunda*. (A, B) metatibia, lateral view; (C–E) apex of metatibia, medial view; (F, G) apex of metatibia, caudal view; (H) aedeagus, ventral view; (J–R) parameres, dorsal view; (S–X) aedeagus, left-side lateral view (not to scale).

Head

1. Labroclypeus: (0) flat (Figs. 1C, E, and F); (1) moderately convex medially (Fig. 1D); (2) with

strong transverse elevation medially (Figs. 1A and B).

2. Labroclypeus, punctation: (0) simple (Figs. 1A, C, and E); (1) rugose (Figs. 1B and D).

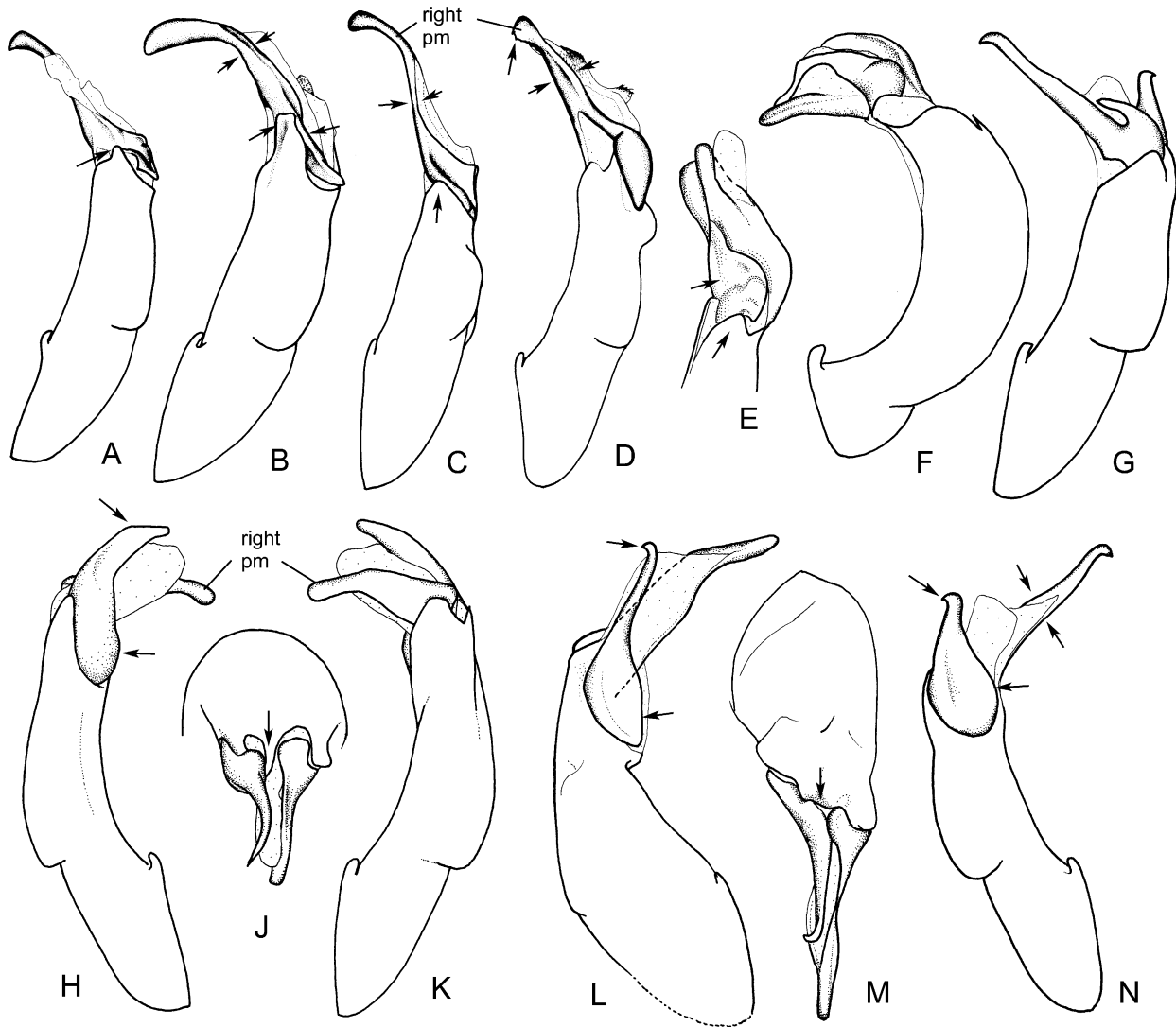


Fig. 3. (A) *Maladera incola*; (B) *M. joachimi*; (C) *M. thakkholae*; (D) *M. simlana*; (E) *M. spectabilis*; (F) *M. taurica*; (G, N) *M. orientalis*; (H–K) *M. cariniceps*, lectotype; (L, M) *M. lignicolor*. (A–D, F, G, K) aedeagus, right-side lateral view; (E) parameres, right-side lateral view; (H, L, N) aedeagus, left-side lateral view; (J, M) parameres, dorsal view (not to scale).

3. Labroclypeus, anterior angles: (0) rounded (Figs. 1A, B, D, and E); (1) bluntly angled (Figs. 1C and F).
4. Labroclypeus, anterior margin medially: (0) distinctly sinuate (Figs. 1A–E); (1) straight.
5. Labroclypeus, lateral margin behind labrum: (0) not incised (Figs. 1A, B, D, and E); (1) incised (Figs. 1C and F); (2) 0 and 1.
6. Labroclypeus anterior angles: (0) simple (Figs. 1A, B, D, and E); (1) strongly reflexed (Figs. 1C and F).
7. Lateral margin of labroclypeus and margin of ocular canthus produced into: (0) distinct angle (Figs. 1A, D, and E); (1) very indistinct angle (Figs. 1B and C).
8. Frons: (0) glabrous (Figs. 1A–E); (1) with transverse row of setae directed posteriorly.
9. Frons: (0) dull (Figs. 1B, C, and F); (1) shiny (Figs. 1A, D, and E).

10. Eyes, size: (0) medium (ratio ocular diameter/interocular width >0.5) (Figs. 1B–E); (1) small (ratio ocular diameter/interocular width <0.5) (Fig. 1A); (2) very large (ratio ocular diameter/interocular width ~0.8).
11. Antenna, number of antennomeres: (0) ten; (1) nine.

Thorax

12. Body, dorsal surface: (0) dull; (1) shiny.
13. Body, coloration of dorsal surface: (0) reddish brown; (1) blackish; (2) dark brown.
14. Mesosternum between mesocoxae: (0) narrow (narrower than mesofemur) (Fig. 1G); (1) wide (wider than mesofemur) (Fig. 1H).

Table 2. Consistency index (CI) and retention index (RI) values calculated by the parsimony ratchet analysis run with WINCLADA/NONA

Character	CI	RI
1	0.28	0.58
2	0.33	0.75
3	0.50	0.75
4	1.0	1.0
5	0.50	0
6	0.50	0.66
7	0.50	0.66
8	0.50	0.80
9	1.0	1.0
10	0.50	0.33
11	0.50	0.66
12	0.50	0
13	0.50	0.80
14	1.0	1.0
15	0.50	0.50
16	0.25	0
17	0.33	0.77
18	1.0	1.0
19	0.50	0.66
20	0.25	0.40
21	0.33	0.50
22	0.50	0.75
23	0.66	0.88
24	0.33	0
25	0.50	0
26	0.33	0.77
27	Uninformative	
28	0.50	0
29	1.0	1.0
30	0.60	0
31	0.40	0.25
32	Uninformative	
33	0.75	0.90
34	0.50	0
35	0.25	0.50
37	0.33	0.77
38	1.0	1.0
39	0.33	0.77
40	1.0	1.0
41	0.66	0
42	0.33	0.71
43	1.0	1.0
44	0.33	0.50
45	1.0	1.0
46	0.50	0.80
47	1.0	1.0

15. Elytra, apical border: (0) glabrous; (1) with rim of fine microtrichomes (Fig. 644 in Ahrens 2004).

Legs

16. Metafemur, posterior margin dorsally: (0) not serrate; (1) serrate.

17. Metafemur, between the two longitudinal hair rows: (0) coarsely punctate; (1) smooth or very superficially punctate.
18. Metafemur, distance between punctures of anterior hair row: (0) small; (1) large; (2) very small.
19. Metatibia, position of basal external group of spines: (0) at one-third or less of the metatibial length (Fig. 2A); (1) at half the metatibial length (Fig. 2B).
20. Metatibia, interior spines on apical face: (0) absent (Fig. 2G); (1) present (Fig. 2F).
21. Metatibia, widest: (0) at apex (Fig. 2B); (1) at middle (Fig. 2A).
22. Metatibia, apex interiorly close to tarsal insertion: (0) bluntly angled, not truncate (Fig. 2E); (1) bluntly angled, slightly concavely sinuate (Fig. 2C); (2) moderately truncate (Fig. 2D).
23. Metatarsomere I in relation to superior spine of metatibia: (0) little longer or equal in length; (1) distinctly longer; (2) twice as long.
24. Metatarsomeres I–IV, pilosity: (0) present (Fig. 1K); (1) absent (Fig. 1J).
25. Tarsi, dorsal punctation: (0) present; (1) absent.
26. Metatarsomeres, subventral carina beside serrated ventral carina: (0) distinct and robust (Fig. 1J); (1) indistinct, very weak (Fig. 1K).

Male genitalia

27. Phallobase: (0) symmetrical (Figs. 2H and J); (1) asymmetrical (Figs. 2K–R).
28. Phallobase, distally: (0) dorsoventrally flattened (Fig. 2S); (1) not dorsoventrally flattened (Figs. 2T–X).
29. Phallobase apically, between insertion of parameres: (0) widely concavely sinuate (Figs. 2J and K); (1) produced medially (Figs. 2L, N–R); (2) produced sublaterally medially (Fig. 2M).
30. Phallobase at right side apically: (0) not produced (Figs. 3C, E–G, and K); (1) weakly but sharply produced ventrolaterally (Figs. 3A and D); (2) strongly produced ventrolaterally (Fig. 3B).
31. Phallobase preapically, dorsal portion: (0) evenly depressed (Figs. 2S, T, and V; Figs. 3F–H, K, L, and N); (1) abruptly depressed (Fig. 2W); (2) not depressed (Fig. 2U; Figs. 3A and B).
32. Parameres: (0) symmetrical (Figs. 2H and J); (1) asymmetrical (Figs. 2K–R).
33. Length relation right/ left paramere: (0) subequal (1:1) (Figs. 2J, K, P, S, and T; Figs. 3E, F, J, and M); (1) left paramere distinctly longer to about half as long as right paramere (max. 2:1) (Fig. 3N); (2) left paramere about four times shorter than right paramere (4:1) (Figs. 2L, R, W, and X); (3) left paramere strongly reduced, more than six times

- shorter than right paramere (6:1) (Figs. 2M, U, and V).
34. Parameres: (0) both simple (Figs. 2J, L–R, T–X; Figs. 3A–E, H–N); (1) both with two or more distally directed lobes (Fig. 3F); (2) right paramere with two or more distally directed lobes (Fig. 3G).
 35. Right paramere, distal apodeme: (0) not shortened (Figs. 2J, K, M, Q–S, W, and X; Figs. 3H, L, and N); (1) shortened (Figs. 2L, N–P, U, and V).
 36. Right paramere, distal apodeme: (0) unarmed (Figs. 2J–M, P–T, W, and X; Figs. 3A–N); (1) armed with small teeth and spines (Fig. 1L; Figs. 2U and V).
 37. Right paramere, basal lobe: (0) absent (Figs. 2J–M); (1) present (Figs. 2N, O, Q, and R).
 38. Right paramere, separate basal plate: (0) absent (Figs. 3A–D, F, G, and K); (1) present (Fig. 3E).
 39. Right paramere: (0) bent ventrally at middle (Figs. 2W and X; Figs. 3B, C, H, K, and L); (1) not bent ventrally, straight (Figs. 2S and V; Figs. 3G and N).
 40. Right paramere: (0) not dorsoventrally flattened basally (Figs. 3A, D–N); (1) dorsoventrally flattened basally (Figs. 3B and C).
 41. Basal lobe of right paramere: (0) evenly widened basally (Figs. 2Q and R); (1) abruptly widened basally and distally subequal in width (Fig. 2O); (2) medially fused with dorsal median process of phallobase (Fig. 2N).
 42. Right paramere, mesally: (0) narrowed, considerably narrower than apex of phallobase (Figs. 2J, K, and Q); (1) widened, as wide as apex of phallobase (Figs. 2M–O and R).
 43. Basal lobe of right paramere, basally: (0) short and semicircular (Figs. 2O and Q); (1) elongate (Fig. 2R).
 44. Left paramere: (0) straight or bent ventrally at apex (Fig. 2S; Fig. 3H); (1) bent dorsally at apex (Figs. 2T, W, and X; Figs. 3L and N); (2) spherical (Figs. 2U and V).
 45. Left paramere, apically: (0) pointed; (1) rounded.
 46. Insertion of left paramere: (0) at same level as right paramere (Figs. 2J, K, and P); (1) displaced basally (Figs. 2L–O, Q, and R; Figs. 3J and L).
 47. Left paramere, basally: (0) not strongly widened (Figs. 2S–X); (1) strongly widened and convexly elevated (Figs. 3H, L, and N).

Results

The analysis of 47 adult characters with the parsimony ratchet implemented in NONA with the above-mentioned settings yielded 33 equally parsimonious trees of 113 steps (consistency index CI: 0.54, retention index RI: 0.75). Repeating the search ten times yielded the same statistics as above. Characters 27 and 32

resulted as uninformative in the present data set. The strict consensus of these trees, with jackknife values and Bremer support, is presented in Fig. 4. Repeating the parsimony ratchet with modified settings (1000 iterations and ten trees hold per iteration, with ten sequential ratchet runs) did not result in a shorter tree or a modified topology of the strict consensus tree, but it did increase the number of equally parsimonious trees. The tree topology was not affected by altering ACCTRAN or DELTRAN optimization.

The strict consensus (Fig. 4) shows one major monophyletic clade (node A; Bremer support: 3, jackknife value: 92%) within the ingroup, that includes the respective representatives of the subgenera *Cephaloserica* (*M. insanabilis*) and *Omaladera*. However, from the consensus tree, the monophyly of the subgenus *Omaladera* is not evident, due to basal polytomy of the clade which subsequently divides into four lineages (Fig. 4): (1) *M. insanabilis*; (2) node B (*M. spectabilis* + *M. prabangana*); (3) node C (*M. cariniceps*, *M. yasutoshii*, *M. orientalis*, and *M. lignicolor*); and (4) node D containing all Himalayan taxa of *Omaladera*, (*M. stevensi*, *M. gardneri*, (*M. dierli*, *M. sprecheriae* (*M. simlana* (*M. immunda*, *M. emmrichi* (*M. himalayica*, *M. thimphuensis*), (*M. incola* (*M. thakholae*, *M. joachimii*)))))). Due to a limited number of characters available for the analysis and the high level of homoplasy, branch support is generally low (see Fig. 4).

The heuristic search with PAUP 3.1.1. (Swofford 1993) yielded six equally parsimonious trees of 114 steps (CI: 0.54, RI: 0.76) showing a topology very similar to the trees obtained with the NONA parsimony ratchet. The strict consensus tree of the search with equally weighted characters is shown in Fig. 5A. It provides identical principal monophyletic clades (e.g., *Cephaloserica* + *Omaladera*, and monophyletic lineages of the nodes B, C, and D). To assume that the information of the equally parsimonious trees resulted from the parsimony ratchet with equally weighted characters, a majority rule consensus tree was generated (Fig. 6).

To further examine the phylogenetic pattern, the unweighted characters were reanalysed after successive character weighting (Farris 1969) based on the rc index, which resulted in four equally parsimonious trees. Compared to the strict consensus of the original data set, the strict consensus tree from the most parsimonious trees based on successive character weighting shows a slightly different topology. It provides higher resolution in some parts only (Fig. 5B).

Discussion

Both, the majority rule consensus tree from MPTs of the parsimony ratchet and the strict consensus which

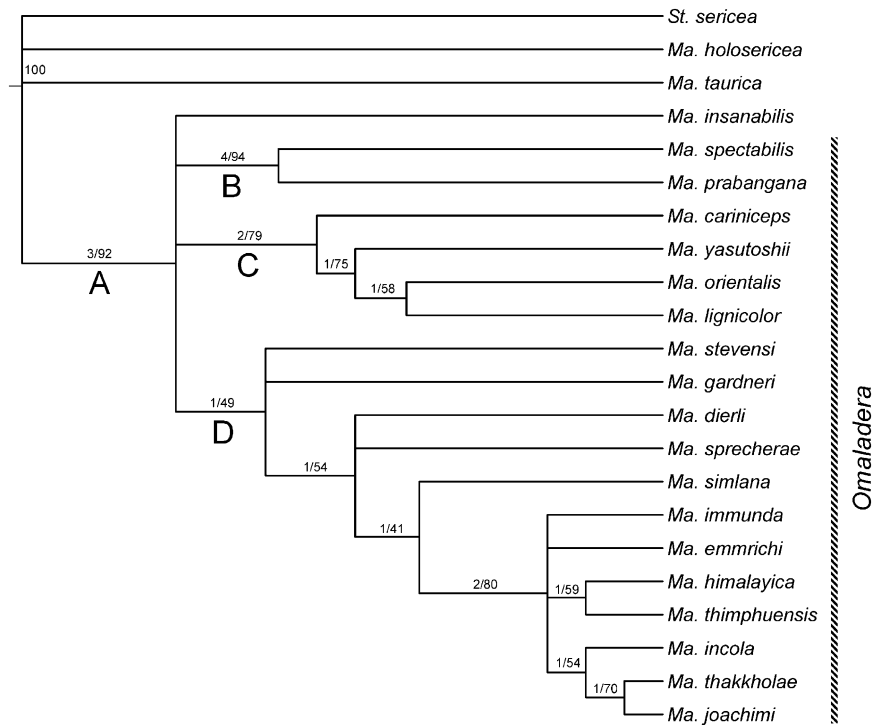


Fig. 4. Strict consensus of the 33 equally parsimonious trees with a length of 113 steps (CI: 0.54; RI: 0.75); support index (Bremer/Jackknife) values above branches. *Ma.* = *Maladera*, *St.* = *Stilbolemma*.

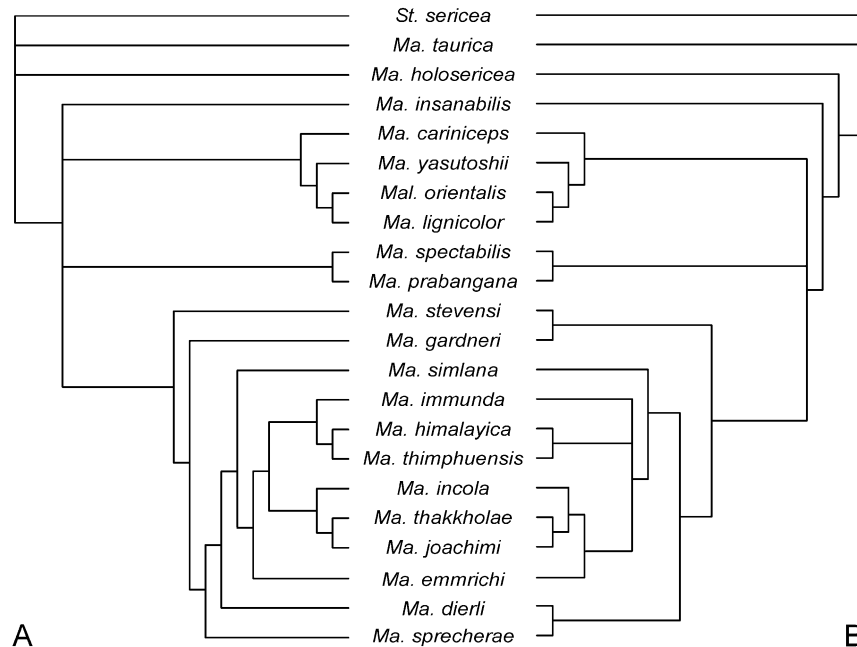


Fig. 5. (A) Strict consensus of six equally parsimonious trees (114 steps; CI: 0.544; RI: 0.765) resulting from heuristic search with PAUP 3.1.1. with unweighted characters. (B) Strict consensus of four equally parsimonious trees resulting from heuristic search with PAUP after successive weighting by the rc index. *Ma.* = *Maladera*, *St.* = *Stilbolemma*.

resulted from heuristic search with PAUP based on successive weighting, were well resolved for (1) the basal relationships, in particular providing evidence for the monophyly of the subgenus *M.* (*Omaladera*) and (2) relationships of the Himalayan taxa of *Omaladera*.

From the 33 equally parsimonious trees generated with the parsimony ratchet (113 steps), which in contrast to the heuristic search with PAUP (114 steps) yielded the shortest tree, one preferred phylogenetic tree was chosen to illustrate character evolution in *Omaladera* (Fig. 7).

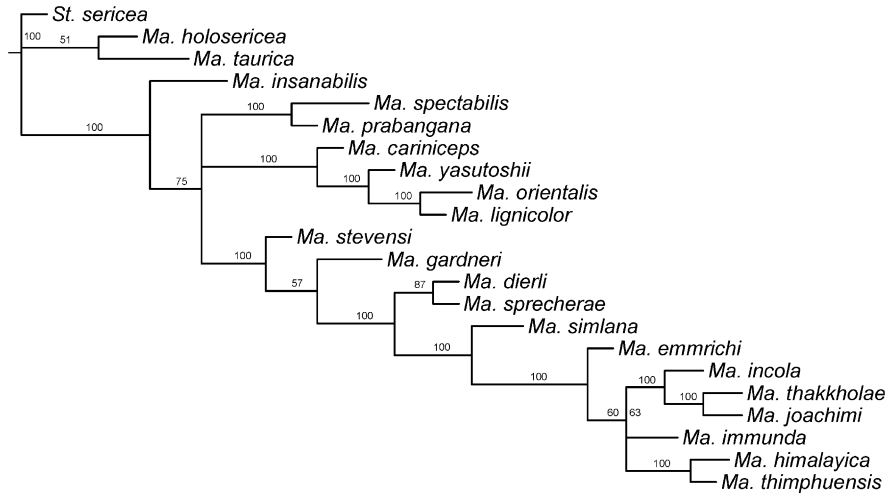


Fig. 6. Majority rule consensus of the 33 most parsimonious trees yielded by the parsimony ratchet (NONA analysis) (113 steps; CI: 0.54; RI: 0.75); numbers above branches indicate % frequency of the respective node among all MPTs. *Ma.* = *Maladera*, *St.* = *Stilbolema*.

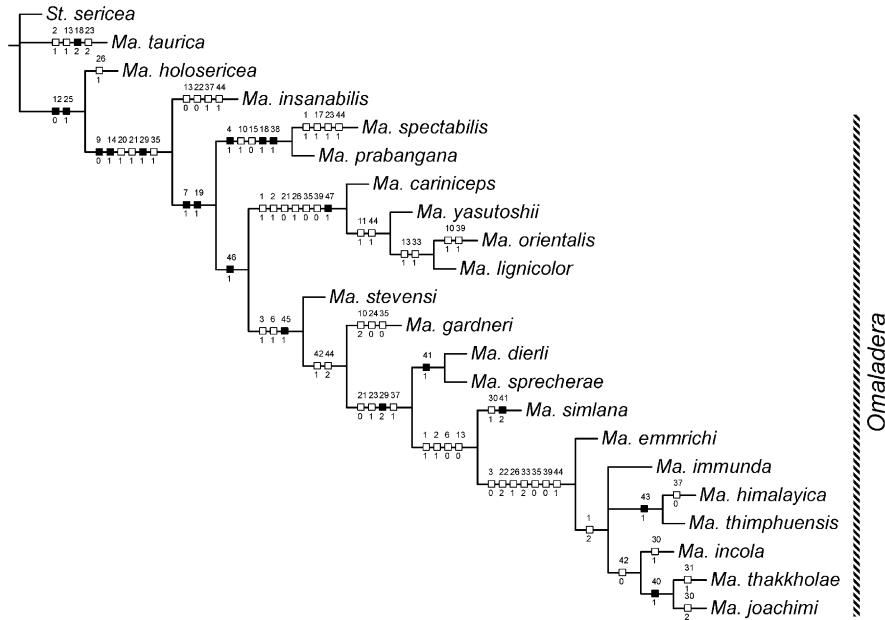


Fig. 7. Preferred tree of the 33 equally parsimonious trees with a length of 113 steps (CI: 0.54; RI: 0.75), showing character changes and apomorphies mapped by state (discontinuous characters mapped as homoplasy; only unambiguous changes shown; unsupported nodes collapsed; proportional branch lengths). The tree was chosen in reference to the majority-rule consensus of the WINCLADA analysis and the strict consensus tree of the PAUP analysis based on successive reweighting. Full squares = non-homoplasious character states, empty squares = homoplasious character states; *Ma.* = *Maladera*, *St.* = *Stilbolema*.

This tree corroborates the majority rule consensus tree derived from the parsimony ratchet and the strict consensus that resulted from heuristic search based on successive weighting with PAUP.

The tree topology of the majority rule consensus tree (Fig. 6) as well as the strict consensus tree obtained after heuristic search with reweighted characters (Fig. 5B) provides support for the hypothesis that the subgenus *Omaladera* is a monophyletic group. The subgenus was established by Reitter (1896) for two species, *M. diffinis*

(Reitter 1896) and *M. cavifrons* (Reitter 1896), whose names are currently regarded as synonymous with *M. orientalis* (Motschulsky, 1857). To facilitate classification and identification of the *Maladera* species, additional taxa have since been included in the subgenus (Ahrens 2004). In the framework of the present study, the monophyly of *Omaladera* is supported by the following apomorphies (Fig. 7): (1) lateral margins of labroclypeus and ocular canthus produce a very indistinct angle (Figs. 1B and C; character 7: state 1); (2)

basal external group of metatibial spines at half metatibial length (Fig. 2B; char. 19: 1). The sister relationship of *Omaladdera* with *Cephaloserica* is based on a number of unambiguous apomorphies not affected by homoplasy: (1) frons dull (char. 9: 0); (2) mesosternum between mesocoxae wider than mesofemur (char. 14: 1); (3) phallobase between insertions of parameres produced mesoapically (char. 29: 1).

Maladdera spectabilis and *M. prabangana* constitute a well-supported clade (node B; Bremer support: 4, jackknife value 94%). Both are representatives of a lineage that includes additional taxa known only from Indochina and southern China. These taxa share the following unambiguous and non-homoplasious apomorphies: (1) anterior margin of labroclypeus medially straight (char. 4: 1); (2) distance between punctures of anterior hair row of metafemur large (char. 18: 1); (3) right paramere with separate basal plate (char. 38: 1; Fig. 7). Furthermore, they are characterized (unambiguous apomorphies, but affected by homoplasy) by small eyes (char. 10: 1) and a glabrous apical border of the elytra (char. 15: 0).

A second well-supported clade is the lineage of node C (Bremer support: 2, jackknife value 79%). These species share the basally strongly widened and convexly swollen left paramere (char. 47: 1; Figs. 3H, L, and N) as the only character not affected by homoplasy. The following additional apomorphies support this node: (1) labroclypeus moderately convex medially (char. 1: 1); (2) labroclypeus with rugose punctation (char. 2: 1); (3) metatibia widest at apex (char. 21: 0); (4) distal apodeme of right paramere not shortened (char. 35: 0); and (5) right paramere bent at middle ventrally (char. 39: 0). This clade has a geographical range limited to north-eastern Palearctic Asia (Fig. 9) including all major archipelagos (Taiwan, Japan, Ryukyu Islands) (Nomura 1973). In addition to *M. cariniceps*, *M. yasutoshii*, *M. orientalis*, and *M. lignicolor*, I hypothesize that *M. oshimana okinawana* Nomura, 1964, *M. oshimana oshimana* Nomura, 1962, and *M. oshimana sakishimana* Nomura, 1964, which all have been described from the

Ryukyu Islands, should be assigned to this lineage based on the characters given in their original descriptions and illustrations of the male genitalia. The majority of the species in this clade exhibit strong infraspecific variation, making it more difficult to distinguish between geographic forms (local populations or subspecies) and simple infraspecific variation. Thus, a more detailed examination of the diversification of this lineage is reserved for future studies, after detailed revision of the morphological variation in the group.

Hypothesized monophyly of the Himalayan *Omaladdera* species clade results from all four approaches of tree search involved in this study, and it is based on the following unambiguous apomorphies: (1) anterior angles of labroclypeus bluntly angled (char. 3: 1); (2) anterior angles of labroclypeus strongly reflexed (char. 6: 1); and (3) left paramere apically rounded (char. 45: 1). Additionally, in the preferred most parsimonious tree (Fig. 7) monophyly is supported by another apomorphy under ACCTAN optimization criterion (Fig. 8A): (4) left paramere about four times shorter than right paramere (char. 33: 2). The reduction of the length of the left paramere in the Himalayan *Omaladdera* species is unique for the Sericini. Based on the scheme of character evolution in Fig. 8A, which resulted from hypothesized phylogeny, the left paramere is shortened even further (char. 33: 3) to more than six times the right paramere. This step, however, is subject to a subsequent reversal (under ACCTAN optimization; Fig. 8A, right circle), whereas under DELTRAN optimization, the strongly shortened left paramere (char. 33: 2) results as having developed twice (Fig. 8B, circles,) in *M. stevensi* and in the clade (*M. emmrichi* (*M. immunda*, (*M. himalayica*, *M. thimphuensis*), (*M. incola* (*M. thakholae*, *M. joachimi*))).

Implications on taxonomy, evolution, and biogeography

Although the current stage of exploration of the Asian sericine fauna is still incomplete (with the

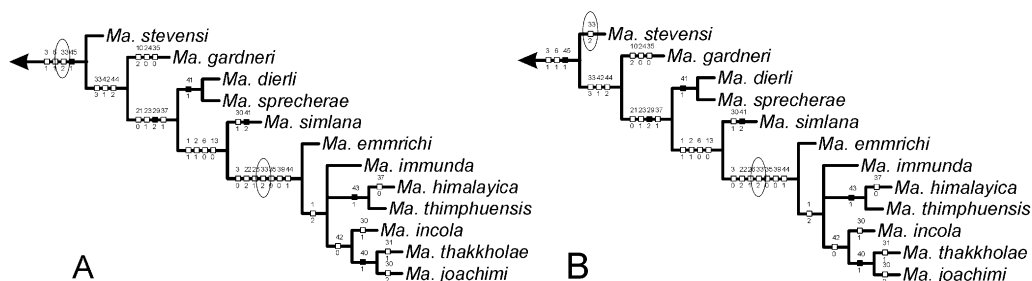


Fig. 8. Character conflict between ACCTAN and DELTRAN optimization in the preferred tree of the 33 equally parsimonious trees (113 steps; CI: 0.54; RI: 0.75), showing apomorphies mapped by state (discontinuous characters mapped as homoplasy, unsupported nodes collapsed; proportional branch lengths). Full squares = non-homoplasious character states, empty squares = homoplasious character states; *Ma.* = *Maladdera*.

exception of the Nepal Himalayas), the records and taxonomic knowledge have improved notably in the last decade (Ahrens, unpublished data). These investigations provide no evidence that the cumulative geographical ranges of the taxa in the three lineages (Fig. 9) of *Omaladera* overlap significantly. Within each of the three regions depicted in Fig. 9 the corresponding lineage diversified independently, and the present phylogenetic hypothesis (Figs. 4–7) is not consistent with a faunal exchange in history concerning the extant representatives or taxa of the stem lineage of each of the three clades.

To understand the main far-reaching factors for the Himalayan diversification, the altitudinal distribution of

the species has to be considered. All species occur within a range from 300 to 3300 m (Fig. 10), i.e., from the hilly to the upper montane zone. However, the interval from 1100 to 2800m is the preferred habitat, based on altitudinal abundance of specimens (Fig. 10). The species are absent in the lowlands below 300m, thus explaining a barrier against direct dispersal from the Himalayas to the climatically similar Khasi Hills in Meghalaya (India) through the lowlands. Based on this altitudinal distribution pattern, taxa of the clade would become permanently separated by mountain ranges higher than 4000m once this altitudinal distribution pattern is established. Such a geographical limit we presently encounter in the Great Himalayan range, e.g.,

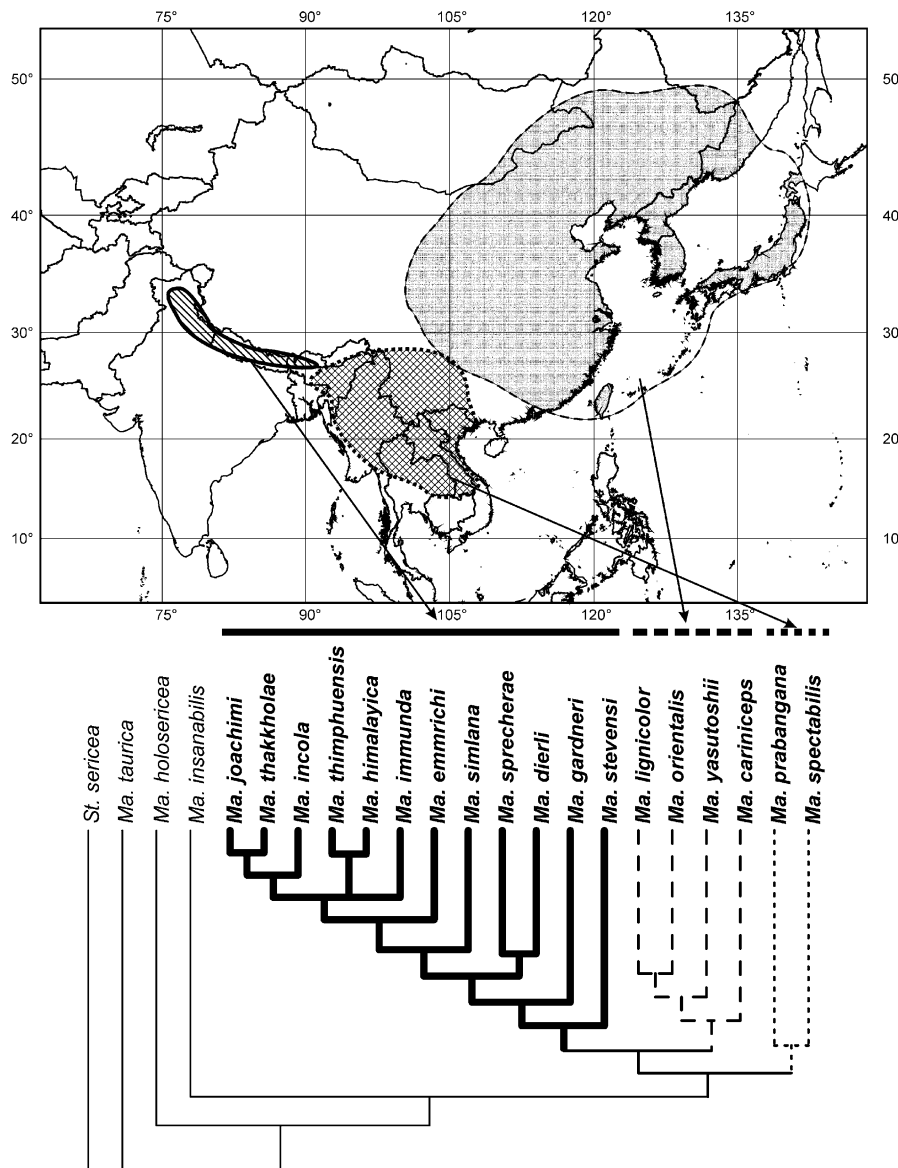


Fig. 9. Hypothesized phylogeny of the subgenus *Omaladera* (based on the preferred most parsimonious tree, Fig. 7) in geographical context, showing the separate occurrence of the three main clades in the Himalayas, Indochina, and North Asia, respectively. *Ma.* = *Maladera*, *St.* = *Stilbolemma*.

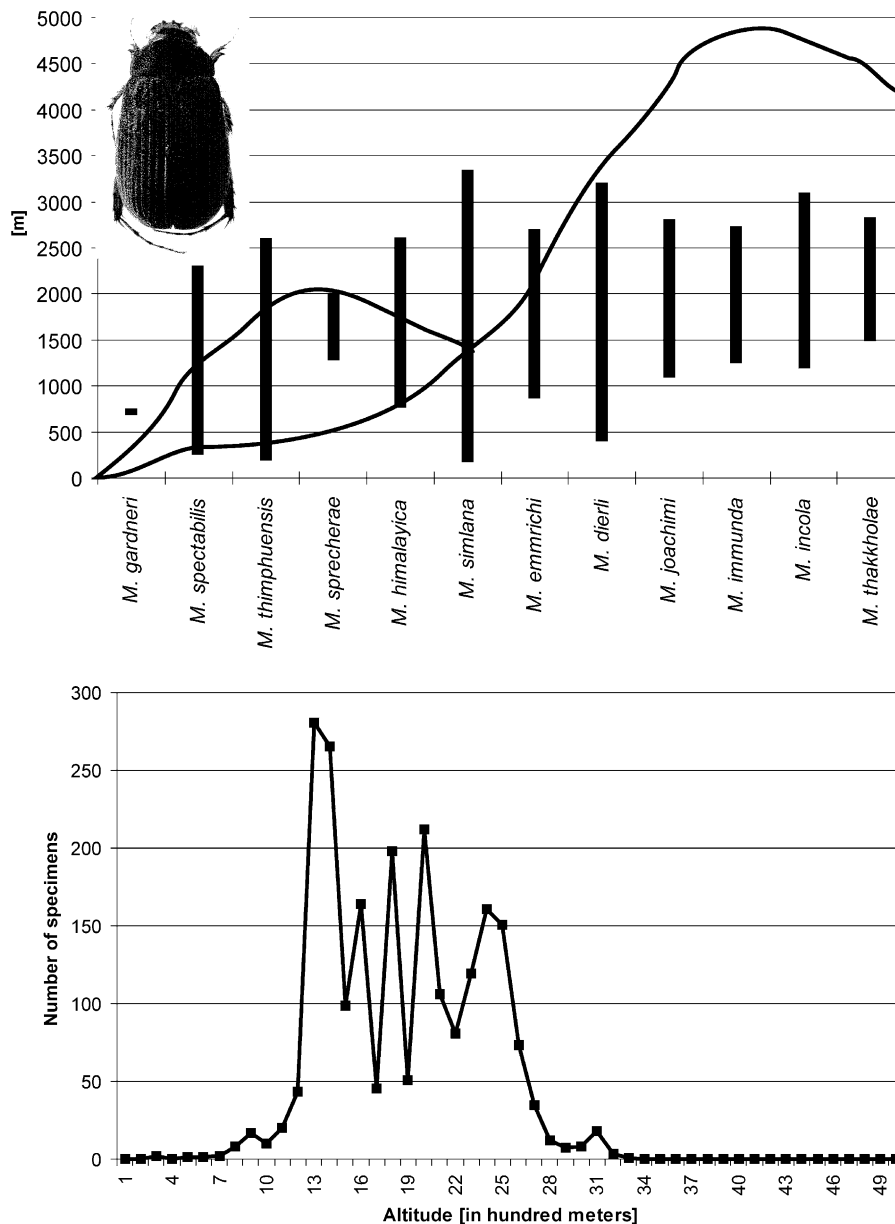


Fig. 10. Altitudinal distribution of Himalayan taxa of the subgenus *Omaladera*, showing (at top) entire record data interval (*M.* = *Maladera*) and (at bottom) total abundance in relation to altitude (in 100 m steps) cumulated over all Himalayan representatives of *Omaladera*; *M. stevensi* not included due to lack of exact altitudinal data for the specimens sampled.

in the Tibetan Plateau as well as in its eastern chains from Gansu (China) in the North to Yunnan (China) and northern Myanmar in the South. The onset of orogeny in these regions is hypothesized to have occurred in the late Eocene (Tapponier et al. 2001). Reaching sufficient height, these ranges must have become geographic barriers for dispersal. Such high elevations could have been achieved during the early Miocene already, as fossil leaf assemblages provide evidence that the altitude in parts of the southern Tibetan Plateau probably has remained unchanged for the past 15 Ma (Spicer et al. 2003). This could be considered as a minimum age for the Himalayan

lineage (Fig. 4, node D), whose splitting (Fig. 7) from the northern Asian lineage (including *M. orientalis*, etc.) (Fig. 4, node C) is consistent with such a separation event.

High relief energy and strong climatic contrast (Dobremez 1976) presumably induced separation processes in periods of fluctuating climate, which must have affected the fauna and flora of the southern Himalayan slope with a hilly montane distribution, such as the taxa of *Omaladera*. Nevertheless, the size of distributional ranges of taxa in the Himalayan *Omaladera* lineage varies greatly: the two basally branching taxa, *M. stevensi* and *M. gardneri*, have very

restricted distribution, whereas the taxa in the more apical lineages have more extensive ranges in the entire central and western Himalayas (e.g., *M. simlana*, *M. dierli*, and *M. emmrichi*). Taxa with more distal positions in the tree are each geographically limited to a small number of mountain massifs or valleys that are separated by deeply incised river valleys or high mountains.

Some of these distal *Omaladera* species are strictly parapatric, which is why they were established originally as subspecies (Ahrens 2004). However, phylogenetic analyses support the hypothesis that *M. himalayica*, *M. incola*, *M. immunda*, and *M. thakholae* are valid species. Corroborative evidence includes the range overlap and syntopic occurrence of the two distal sister taxa, *M. joachimi* and *M. thakholae* (Fig. 11), indicating that also all taxa of their basal lineages (*M. immunda*, *M. incola*, and the last common ancestor of *M. himalayica*+*M. thimphuensis*) must be separate species. Conversely, the present data set and tree topology provide no basis for discussing the status (species or subspecies) of *M. himalayica* and *M. thimphuensis*. Further phylogenetic research based

on molecular data and molecular dating, and additional morphological specimens from the geographical area between the known ranges of the two taxa may be necessary to understand the speciation of *M. himalayica* and *M. thimphuensis*.

Faunistic exploration in the Himalayas is far from complete, and conclusions regarding the “endemic” basal lineages (*M. stevensi*, *M. gardneri*) should be considered only in relation to historical distributions. These hypothesized extensive, Himalayan-wide distributions of stem lineage representatives of the Himalayan *Omaladera* and its basal taxa would be consistent with an evolutionary scenario for *Omaladera* explaining the separate development of the three principal lineages by geographical separation (Fig. 9).

Based on the hypothesized phylogeny of the apical lineages within the Himalayan *Omaladera* clade (Fig. 11), there is support that parapatric speciation played a dominant role during the process of diversification. In contrast to other Himalayan Sericini, the degree of endemism in *Omaladera* is relatively low. This may correspond with the wide ecological tolerances of most species in the group.

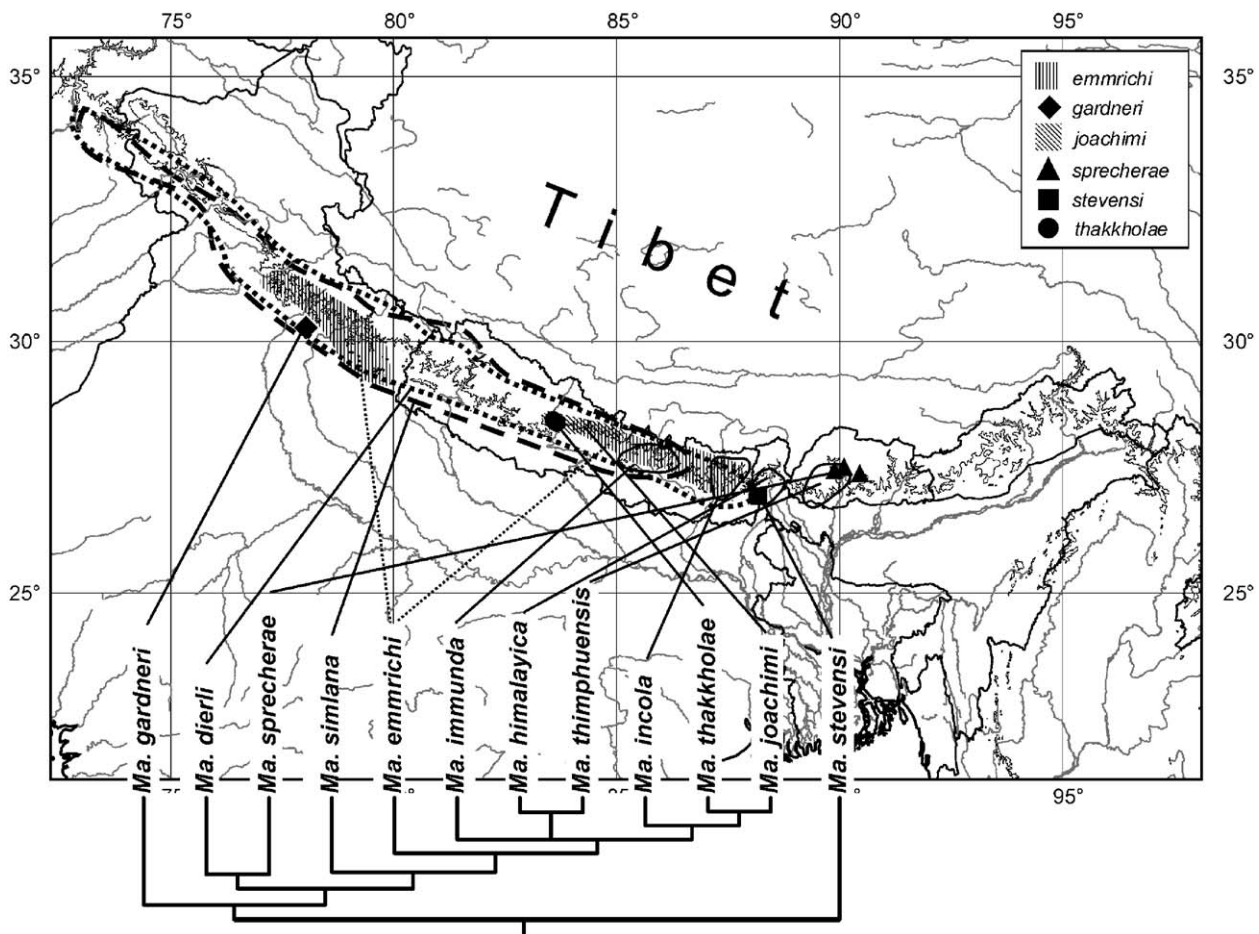


Fig. 11. Phylogenetic tree for Himalayan taxa of the subgenus *Omaladera*, and their respective distribution ranges (*Ma.* = *Maladera*).

Diversification of Himalayan *Omaladera* shows that the Himalayas not only are a region acting as a faunal bridge (Kurup 1990) but rather “recently” invaded and occupied by an “immigrated fauna” (Martens 1993). Based on the phylogeny of *Omaladera*, it must be supposed that parts of the Himalayan fauna (with reference to an altitudinal gradient) have had a rather independent history for a rather long period. In fact, such a hypothesis would be consistent with some of the chorological classification concepts of comparative biogeographers (e.g., summarized in Mani 1974a,b; de Lattin 1967; Dobremez 1976; Martens 1993) establishing a “Himalayan” subcentre or sub-region, respectively, in its own right. When explaining and conserving the rich biodiversity in the Himalayas, responsible attention must be paid not only to the fact that the region lies between the Palearctic and Oriental realms, but also forms a borderline with a high vertical and horizontal faunal interchange. Moreover, it constitutes an autochthonous heritage of great importance.

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Appendix A

Checklist for the subgenus *Maladera* (*Omaladera*), including synonyms

Maladera subgenus *Omaladera* Reitter, 1896

Omaladera Reitter, 1896: 188.

Type species: *Amaladera diffinis* Reitter, 1896 (designated by Ahrens 2004).

Maladera (*Omaladera*) *cariniceps* (Moser, 1915)

Autoserica cariniceps Moser, 1915: 341.

M. (Omaladera) dierli (Frey, 1969)

Cephaloserica dierli Frey, 1969: 522.

M. (Omaladera) fusiana (Murayama, 1934)

Aserica fusiana Murayama, 1934: 35.

M. (Omaladera) emmrichi Ahrens, 2004

Maladera emmrichi Ahrens, 2004: 227.

M. (Omaladera) gardneri Ahrens, 2004

Maladera gardneri Ahrens, 2004: 216.

M. (Omaladera) himalayica (Brenske, 1896)

Autoserica himalayica Brenske, 1896: 152.

M. (Omaladera) immunda Ahrens, 2004

Maladera himalayica immunda Ahrens, 2004: 222.

M. (Omaladera) incola Ahrens, 2004

Maladera himalayica incola Ahrens, 2004: 223.

M. (Omaladera) joachimi Ahrens, 2004

Maladera joachimi Ahrens, 2004: 229.

M. (Omaladera) laboriosa (Brenske, 1897)

Autoserica laboriosa Brenske, 1897: 399.

M. (Omaladera) lignicolor (Fairmaire, 1887)

Serica lignicolor Fairmaire, 1887: 110.

M. (Omaladera) orientalis (Motschulsky, 1857)

Serica orientalis Motschulsky, 1857: 33.

Amaladera cavifrons Reitter, 1896: 188

Amaladera diffinis Reitter, 1896: 188.

Serica famelica Brenske, 1897: 391.

Serica pekingensis Brenske, 1897: 366.

M. (Omaladera) oshimana okinawana Nomura, 1964

Maladera oshimana okinawana Nomura, 1964: 51.

M. (Omaladera) oshimana oshimana Nomura, 1962

Maladera oshimana Nomura, 1962: 38.

M. (Omaladera) oshimana sakishimana Nomura, 1964

Maladera oshimana sakishimana Nomura, 1964: 51.

M. (Omaladera) prabangana (Brenske, 1899)

Autoserica prabangana Brenske, 1899: 414.

M. (Omaladera) simlana (Brenske, 1898)

Autoserica simlana Brenske, 1898: 302.

M. (Omaladera) spectabilis (Brenske, 1898)

Autoserica spectabilis Brenske, 1898: 331.

M. (Omaladera) sprecheriae Ahrens, 2004

Maladera sprecheriae Ahrens, 2004: 214.

M. (Omaladera) stevensi Ahrens, 2004

Maladera stevensi Ahrens, 2004: 231.

M. (Omaladera) thakholae Ahrens, 2004

Maladera himalayica thakholae Ahrens, 2004: 225.

M. (Omaladera) thimphuensis Ahrens, 2004

Maladera himalayica thimphuensis Ahrens, 2004: 220.

M. (Omaladera) yasutoshii Nomura, 1974

Maladera yasutoshii Nomura, 1974: 104.

Appendix B

Morphological character matrix used for the analysis

Character number	1	111111112	222222223	333333334	4444444
Species	1234567890	1234567890	1234567890	1234567890	1234567
<i>St. sericea</i>	200000011	1120010000	0101000000	0000000010	- 0-000?
<i>Ma. cariniceps</i>	1100001100	0021100011	0101111110	0100000000	- 0-0011
<i>Ma. dierli</i>	0010111000	0021111011	0111101120	2130111010	1102110
<i>Ma. emmrichi</i>	1100001000	0001101011	0211111120	2120001000	0101110
<i>Ma. gardneri</i>	0010111002	0021110010	1000101110	0130000010	- 1-2110
<i>Ma. himalayica</i>	2100001000	0001101011	0211111120	0120000000	0111110
<i>Ma. holosericea</i>	0000000010	0020100000	0100111000	0101000010	- 0-0000
<i>Ma. immunda</i>	2100001000	0001101011	0211111120	0120001000	0101110
<i>Ma. incola</i>	2100001000	0001101011	0211111121	2120001000	0001110
<i>Ma. insanabilis</i>	0000000000	0001100001	1001101110	0100101010	0001000
<i>Ma. joachimi</i>	2100001000	0001101011	0211111122	2120001001	0001110
<i>Ma. lignicolor</i>	1100001100	1011100011	0101111110	0110000000	- 0-1011
<i>Ma. orientalis</i>	1100001101	1011100011	0101111110	0112000010	- 0-1011
<i>Ma. prabangensis</i>	0001001101	0021000111	1101101110	0100100110	- 0-0000
<i>Ma. simlana</i>	1110201000	0001101011	0111101121	0130111010	2102110
<i>Ma. spectabilis</i>	1001001101	0021001111	1111101110	0100100110	- 0-1000
<i>Ma. sprecheriae</i>	0010111000	0021111010	0111101120	2130111010	1102110
<i>Ma. stevensi</i>	0010011000	0021101010	1001101110	0120100010	- 0-0110
<i>Ma. taurica</i>	1100000010	0110100200	0120001100	0101000010	- 0-0000
<i>Ma. thakkholae</i>	2100001000	0001101011	0211111120	1120001001	0001110
<i>Ma. thimphuensis</i>	2100001000	0001101011	0211111120	0120001000	0111110
<i>Ma. yasutoshii</i>	1100001100	1021100011	0101111110	0102000000	- 0-1011

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