

Cladistic analysis of *Sericania* (Coleoptera: Scarabaeidae: Sericini) – implications for the evolution of the xerophilous fauna of the Himalaya

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Abstract. A cladistic analysis of the species of *Sericania* Motschulsky, 1860, was executed using fifty-six morphological characters of adults. The monophyly of the genus is supported by the phylogenetic trees generated. Among the three major lineages indicated by the strict consensus tree the East Asian *Sericania fuscolineata* lineage represents the genus *Sericania* as defined “originally” and adopted by subsequent authors. The second, the clade *Sericania nepalensis* group + *Sericania* sp. 2, is a sister group to the *S. fuscolineata* clade. Both constitute a sister group to the third major lineage, the *Sericania kashmirensis* clade, which is endemic in the drier North-West Himalaya where it is the most diverse monophyletic group of Sericini. Provided that the stem species of the *S. kashmirensis* clade was xerophilous, the origin of this clade can not predate the early Miocene. Based on paleoclimatical and geological data, two competing hypotheses are proposed to explain the evolution of the xerophilous *Sericania* lineage: (a) a basal splitting within *Sericania* occurred because of the altitudinal and climatic barrier posed by the Himalaya, which separated the xerophilous lineage in the north (Tibet) from the hygrophilous lineage in the south-east (S slope of Himalaya/ Tibet), or (b) it was a consequence of the increase in the climatic east-west contrast along the southern slope of the Himalaya, which strengthened with the onset of monsoons 8 Ma ago.

INTRODUCTION

Since the breaking up of Gondwana tectonic and orogenic processes have influenced climate and evolution in South Asia. The accretion of the Indian plate and its subduction under the Asian plate led not only to extensive volcanism and orogenesis but also changed extensively the distribution of sea and land, which caused modifications in wind circulation and consequently the climate in Asia (Ramstein et al., 1997).

The most recent attempts (e.g. Dobremez, 1976; Martens, 1983, 1993) to investigate the patterns of biodiversity in the Himalayan orogenic belt, reveal a trend in impoverishment of the fauna and flora along the Himalayan chain from east to west. This trend also occurs in the beetle tribe Sericini. For any investigation of the evolution of the Himalayan fauna important information may be provided by subordinate patterns, such as those found in many xerophilous forms, invading the Himalaya from the west (Mani, 1968; Martens, 1993) and becoming dominant elements of the fauna and flora of the alpine belt. However, alpine elements appear to be missing among the Sericini (Ahrens, 2004). The upper altitudinal occurrence of Sericini is limited by the absence of a soil layer with humus and plant roots. For that reason, these beetles have not occupied high altitudes.

Although very poor in terms of species richness, a similar general pattern of xerophilous organisms is reported among the montane forms of Sericini (Ahrens, 2004), which achieved in the NW Himalaya a higher

diversity than in other regions of the Himalaya. One of these groups is the genus *Sericania*, with one major lineage (*S. kashmirensis* group) occurring in the montane belt of North-West Himalaya of which some species extend their ranges further east into the central Himalaya.

Sericania is with 65 known species a comparatively diverse sericine taxon. The taxonomy and distribution of the Himalayan species was revised recently (Ahrens, 2004) and the taxa of the Asian mainland were reviewed by Nomura (1976). The cladistic analysis presented here was conducted to further the understanding of the effect of factors such as orogenesis, climate shifting or glaciation on evolution of organisms and in particular improve our knowledge of the relationships among the Sericini.

MATERIAL AND METHODS

Taxon sampling and characters

Thirty-three species belonging to six genera were included in the cladistic analysis, with *Pleophylla* sp. as the outgroup because they are closely related but not part of the ingroup taxa (Ahrens, 2006).

Description, coding and illustration of characters was based on the 36 species belonging to six genera listed in Table 1. The material used in this analysis originated mainly from the author's collection (CA) with additional specimens borrowed from the following collections: Deutsches Entomologisches Institut, Müncheberg (DEI); Staatliches Museum für Naturkunde, Stuttgart (SMNS); Hungarian Natural History Museum, Budapest (HNHM); Muséum d'histoire naturelle, Genève (MHNG); Naturhistorisches Museum, Basel (NHMB);

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TABLE 1. List of the species studied for the cladistic analysis († not included in the analysis).

Species	Distribution	Depository
<i>Pleophylla</i> Erichson, 1847 spec.	Southern Africa	CA
<i>Maladera holosericea</i> (Scopoli, 1772)†	Europe, Siberia	CA
<i>Nepaloserica procera procera</i> Frey, 1965	Nepal	CA
<i>N. goomensis</i> Ahrens, 1999†	Darjeeling	CA
<i>N. procera rufescens</i> Frey, 1965†	Nepal	CA
<i>Nipponoserica koltzei</i> Reitter, 1897	Manchuria, Korea	CA
<i>Stilbolema sericea</i> (Illiger, 1802)†	USA, Canada	CA
<i>Chrysoserica auricoma</i> (Brenske, 1896)	Himalaya to northern Indochina	CA
<i>Sericania babaulti</i> Ahrens, 2004	NW Himalaya	MNH, CA
<i>S. besucheti</i> Ahrens, 2004	NW Himalaya	MHNG
<i>S. bhojpurensis</i> Ahrens, 2004	Eastern Nepal	SMNS
<i>S. carinata</i> Brenske, 1898	? NW Himalaya	ZMHB
<i>S. costulata</i> (Moser, 1915)	W Himalaya	ZMHB, CA
<i>S. dispar</i> Ahrens, 2004	NW Himalaya	NHMB
<i>S. dubiosa</i> Ahrens, 2004	NW Himalaya	NHMB
<i>S. fuscolineata</i> Motschulsky, 1860	North-Eastern China	CA
<i>S. gilgitensis</i> Ahrens, 2004	NW Himalaya	NHMB, CA
<i>S. hazarensis</i> Ahrens, 2004	NW Himalaya	NHMB, CA
<i>S. heinzi</i> Ahrens, 2004	NW Himalaya	CA
<i>S. kashmirensis</i> (Moser, 1919)	NW Himalaya	ZMHB, CA
<i>S. khagana</i> Ahrens, 2004	NW Himalaya	HNHM
<i>S. kleebergi</i> Ahrens, 2004	Central Nepal	BMNH, CA
<i>S. laeticula</i> (Sharp, 1878)	NW Himalaya	NHMB, CA
<i>S. lewisi</i> Arrow, 1913	Japan	CA
<i>S. loebli</i> Ahrens, 2004	NW Himalaya	MHNG
<i>S. mara</i> Ahrens, 2004	Central Nepal	CA
<i>S. mela</i> Ahrens, 2004	Central Nepal	CA
<i>S. nepalensis</i> (Frey, 1965)	Central Nepal	CA
<i>S. pacis</i> Ahrens, 2004	NW Himalaya	MNH
<i>S. piattellai</i> Ahrens, 2004	NW Himalaya	MSNG
<i>S. poonchensis</i> Ahrens, 2004	NW Himalaya	SMTD
<i>S. swatensis</i> Ahrens, 2004	NW Himalaya	MHNG
<i>S. torva</i> Ahrens, 2004	NW Himalaya	MHNG, HNHM
<i>S. yamauchii</i> Sawada, 1938	Japan-Ussuri	CA
<i>Sericania</i> sp. 1	Tatsienlu (Sichuan, China)	SMTD
<i>Sericania</i> sp. 2	Ta-pai Shan (Shaanxi, China)	ZMHB

Staatliches Museum für Tierkunde, Dresden (SMTD); Zoologisches Museum der Humboldt-Universität, Berlin (ZMHB). The choice of taxa included in the ingroup was mainly based on the current classification of the *Sericania* species (Nomura, 1976) and preliminarily hypothesized relatives (Ahrens, 2004). Fifty-six adult characters were scored. The character states are illustrated in Figs 1 and 2.

Phylogenetic analysis

The 56 characters (40 were binary and 16 multistate) were all treated as unordered and equally weighted. Inapplicable characters were coded as “–”, while unknown character states were coded as “?” (Strong & Lipscomb, 1999). The parsimony analysis was performed in NONA 2.0 (Goloboff, 1999) using the parsimony ratchet (Nixon, 1999) implemented in NONA with WINCLADA vs. 1.00.08 (Nixon, 2002) as a shell program. Two hundred iterations were performed (one tree held per iteration).

repeating the search ten times. The number of characters resampled during the parsimony ratchet was determined to be five. All searches were done under the collapsing option “ambiguous”, which collapses every node with a minimum length of 0. State transformations were considered to be apomorphies of a given node only if they were unambiguous (i.e., without arbitrary selection of accelerated or delayed optimization) and if they were shared by all dichotomised most parsimonious trees.

The use of resampling methods (particularly the bootstrap) is questioned as a means of assessing confidence limits of phylogenies (Carpenter, 1992, 1996; Kluge & Wolf, 1993). This is principally because these tests rely on the assumption that the characters are “independently and identically distributed” (Felsenstein, 1985) and that they have been randomly sampled – two assumptions violated by most phylogenetic data. Morpho-

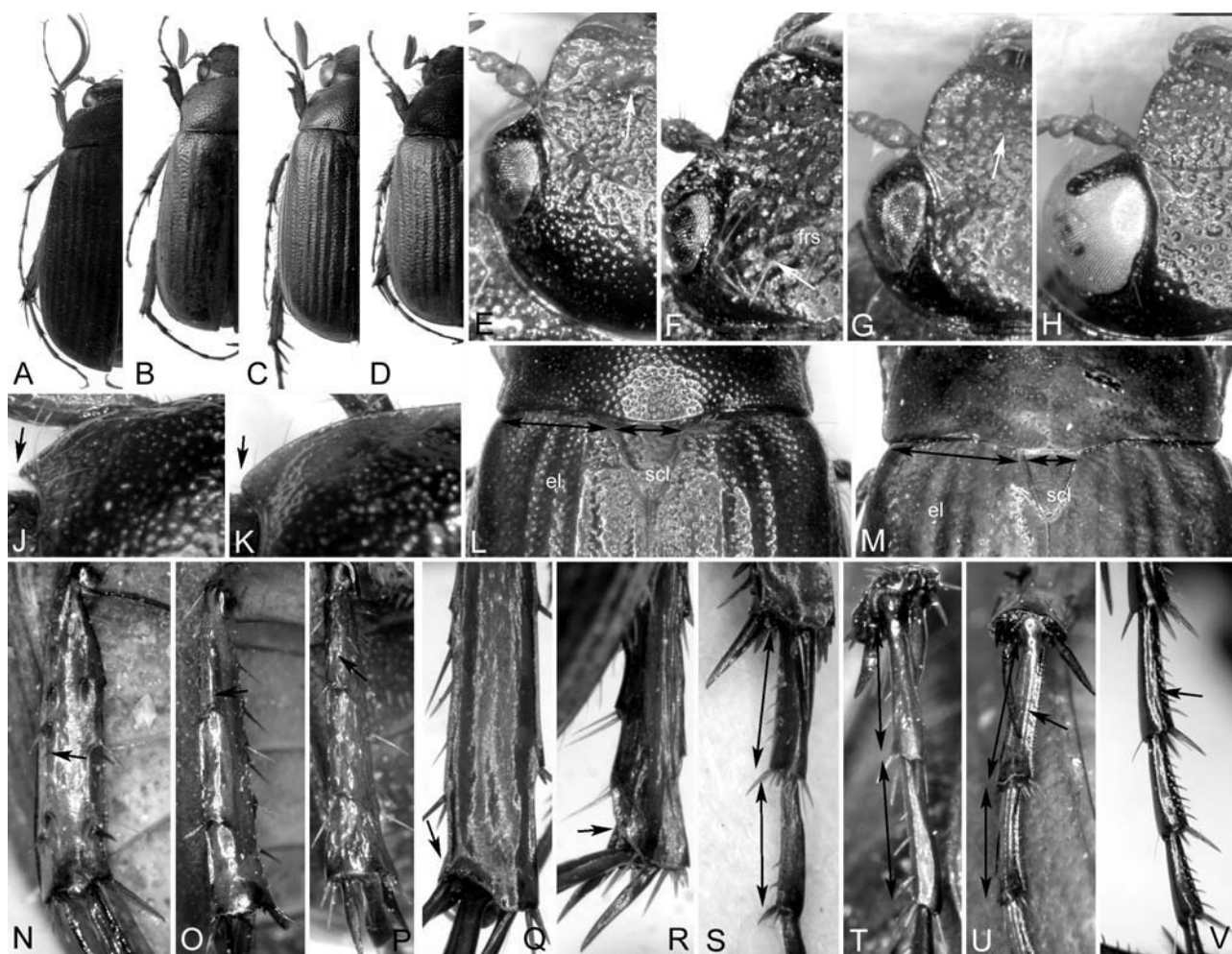


Fig. 1. A – *Nepaloserica goomensis*; B – *Sericania mara*; C, H, L – *S. laeticula*; D, F, J, S – *S. piattellai*; E, K, P, R, T – *S. fusco-lineata*; G – *S. khagana*; M – *S. yamauchii*; N, U – *Nipponoserica koltzei*; O, Q – *N. procera rufescens*; V – *Maladera holosericea*. A–D – habitus, dorsal view; E–H – head, dorsal view; J, K – pronotum, right half, dorsal view; L, M – pronotum, scutellum, and elytral base, dorsal view; N – metatibia, lateral view; O, P – metatibia, dorsolateral view; Q, R – metatibia, medial view (detail); S–V – basal metatarsomeres, (S – medial view, T–V – lateral view) (not to scale).

logical data sets are particularly susceptible to these problems as they are often replete with examples of redundant (inapplicable) and correlated characters, although molecular data sets are not immune from this (e.g. ribosomal RNA genes, which code for a secondary structure). However, as an estimate of the robustness of a data set, these resampling techniques can be useful for discovering ambiguity between characters.

Bremer support (Bremer, 1988, 1994) and bootstrap values (Felsenstein, 1985) were evaluated using NONA. Bootstrap analyses of data were performed with 200 replicates using TBR branch swapping. The bootstrap values did not augment significantly when uninformative characters were deleted from the matrix. The search was set to a Bremer support level of 12, 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. Character changes were mapped on the consensus tree using WINCLADA.

Successive weighting (Farris, 1969) was used to evaluate further phylogenetic relationships. This method uses *post hoc* character weighting based on the fit of each character as applied to the trees currently in the 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 ana-

lysing phylogenetic pattern when characters exhibit a high level of homoplasy. Characters were reweighted based on the consistency index. The base weight was set at 100. Weights were inserted manually into NONA parsimony ratchet search via WINCLADA. 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 hypothesis about their transformation. In particular, coding does not imply whether a state is derived or ancestral. The data matrix is presented in Table 2.

Head

1. Surface of the body: (0) with dull cover of microtrichomes (Fig. 1A); (1) shiny, without dull cover of microtrichomes (Fig. 1B–D).
2. Body, colour: (0) head + pronotum of the same colour as elytra (Fig. 1A–C); (1) head + pronotum of different colour to elytra (Fig. 1D).
3. Body, colour of ventral face: (0) reddish or dark brown; (1) yellowish; (2) black.

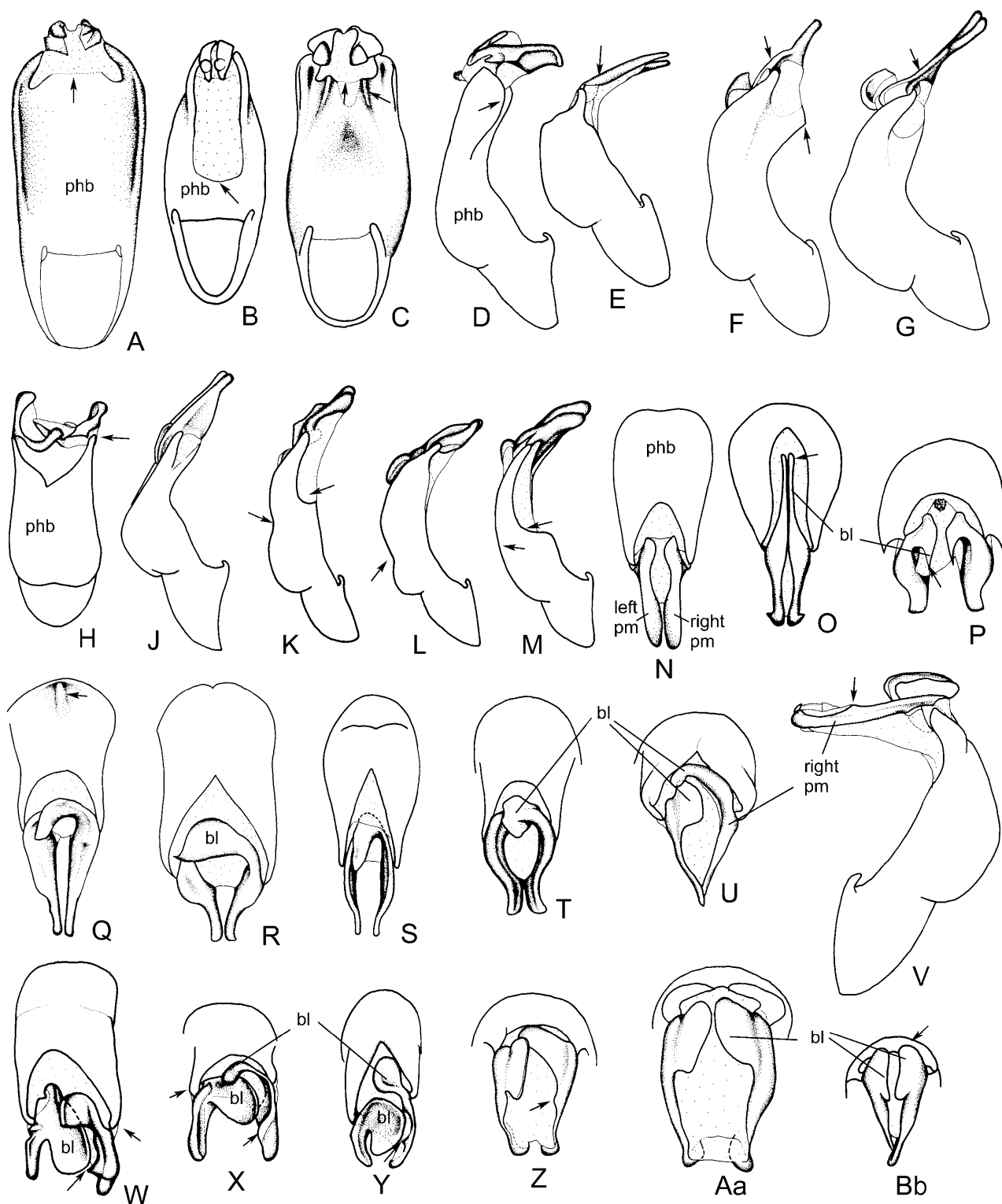


Fig. 2. A – *Nepaloserica goomensis*; B, O – *Nipponoserica koltzei*; C – *S. piattellai*; D, P – *S. gilgitensis*; E, U – *S. yamauchi*; F, R – *S. poonchensis*; G, Q – *S. besucheti*; H, M, X – *S. kleebergi*; J, S – *S. costulata*; K – *S. mela*; L, Y – *S. nepalensis*; N – *Stilbolema sericea*; T – *S. dubiosa*; V, Aa – *Sericania* sp. 1; W – *S. mara*; Z – *S. lewisii*; Bb – *Sericania* sp. 2. A–C – aedeagus, ventral view; D–G, J–M – aedeagus, left side lateral view; H – aedeagus, dorsal view; N–U, W–Bb – parameres, dorsal view; V – aedeagus, right side lateral view (not to scale).

4. Anterior margin of labroclypeus medially: (0) distinctly sinuate; (1) very shallowly sinuate.
5. Labroclypeus, basis: (0) completely shiny; (1) dull.
6. Surface of labroclypeus: (0) flat (Fig. 1F, H); (1) convexly elevate medially (Fig. 1G, arrow); (2) transversely elevate medially (Fig. 1E, arrow).
7. Frons: (0) dull; (1) completely shiny.

TABLE 2. Data matrix for the cladistic analysis. Inapplicable characters are coded as “–” and missing character states as “?”. All characters are equally weighted and nonadditive.

Char. number (10)	1111111112	2222222223	3333333334	4444444445	555555
Char. number	1234567890	1234567890	1234567890	1234567890	123456
<i>Pleophylla</i>	1001001100	0301010001	0000200000	00-0-0000-	0100121010 0-0020
<i>Chrysoserica auricoma</i>	0000100000	0101001000	1012211000	1000-0200-	0100101011 000020
<i>Nepalserica procera</i>	0000100020	0411000000	1012211000	0000-0200-	0100120010 000010
<i>Nipponoserica koltzei</i>	0000000000	1000001000	1111211010	0000-0000-	0000101011 100020
<i>Serica brunna</i>	0000000020	1010000100	1012210010	10-0-0000-	211-0----- --0---
<i>Sericania babaulti</i>	1000011001	0110001000	0020110012	000100200-	0110121010 000000
<i>S. besucheti</i>	0000010001	010?001000	0010111012	000100210-	0110121010 000000
<i>S. bhojpurensis</i>	1011011000	1010000100	1000301010	1000-02010	2100112110 000010
<i>S. carinata</i>	1000011001	0100001000	0010111012	0000-0200-	0111121010 100010
<i>S. costulata</i>	1000011001	0100001000	0010111012	0000-0200-	0111121010 100011
<i>S. dispar</i>	1000001021	011?001000	0010111012	000110200-	0111121011 100002
<i>S. dubiosa</i>	1000021001	010?001000	0010111011	0000-0200-	0112121010 000000
<i>S. fuscolineata</i>	1000021000	1201100110	0020300110	0000-0200-	0100120010 001000
<i>S. gilgitensis</i>	1120011111	010?111001	0000110011	010100200-	0002103010 100010
<i>S. hazarensis</i>	2000011001	0100001000	0010111011	100100210-	0110121010 000000
<i>S. heinzi</i>	1000001001	0100001000	0020110011	100100200-	0110102010 000020
<i>S. kashmiriensis</i>	1000001001	0100101000	0020110011	000100200-	0110121010 000000
<i>S. khagana</i>	1000021001	010?001000	0010111011	0000-0200-	0112121010 000000
<i>S. kleebergi</i>	1011011000	1000010100	1000301010	1010-1200-	1100112010 000000
<i>S. laeticula</i>	1000001021	0110001000	0010111011	000110200-	0111121011 100002
<i>S. lewisi</i>	1000001010	1101100110	0020300110	1000-0200-	0100100110 001000
<i>S. loebli</i>	1000011001	010?001000	0010110011	1000-0200-	0112121010 100011
<i>S. mara</i>	1011011000	1000010100	1000301110	1010-12011	2103112110 011000
<i>S. mela</i>	1011011000	1000010100	1000301110	1010-02010	1103112110 011000
<i>S. nepalensis</i>	1011011000	1000010100	1000301110	1010-12011	1103112110 011000
<i>S. pacis</i>	1000001001	0100001000	0010110011	100100200-	011?121010 000000
<i>S. piattellai</i>	1120011111	010?111001	0000110011	010100200-	0002103010 100010
<i>S. poonchensis</i>	1000001021	011?001000	0010111011	100110200-	0111121011 100002
<i>S. swatensis</i>	0000010001	0100001000	0010111011	000100210-	0111121010 000000
<i>S. torva</i>	1000011001	0100001000	0010111012	0000-0200-	0111121010 100011
<i>S. yamauchii</i>	0000010000	110?100110	0010300110	1000-0200-	2100120011 000002
<i>Sericania</i> sp. 1	2000001001	110?101010	1020300210	0000-0200-	0100120110 001100
<i>Sericania</i> sp. 2	1001011020	001?111100	0010300010	0000-0200-	0100100110 000100

8. Frons: (0) with a few single setae behind frontoclypeal suture (Fig. 1E, G, H); (1) completely covered by long setae (Fig. 1F).
9. Eyes in male: (0) medium sized, ratio of diameter/ interocular width ~ 0.7 – 0.5 (Fig. 1E, G); (1) small, ratio of diameter/ interocular width < 0.5 (Fig. 1F); (2) very large, ratio of diameter/ interocular width ~ 0.8 (Fig. 1H).
10. Head, postocular furrow: (0) strong; (1) absent.
11. Total number of antennomeres: (0) ten; (1) nine.
12. Antenna, number of antennomeres of clavus in male: (0) three; (1) four; (2) five; (3) six; (4) seven.
13. Antenna, clavus in male: (0) shorter than total maximal width of labroclypeus (Fig. 1B, D); (1) longer than total maximal width of labroclypeus (Fig. 1A, C).
14. Antenna, number of antennomeres of clavus in female: (0) three; (1) four.

Thorax

15. Pronotum, anterior marginal line: (0) present; (1) absent.
16. Pronotum, anterior angles: (0) blunt and weakly produced (Fig. 1K); (1) sharp and strongly produced (Fig. 1J).

17. Apical margin of elytra: (0) without short microtrichomes; (1) with short microtrichomes.
18. Scutellum in comparison to elytral base: (0) wide (Fig. 1L); (1) narrow (Fig. 1M).

Legs

19. Metacoxa: (0) not transversely impressed; (1) transversely impressed.
20. Metacoxa, ventral surface: (0) glabrous, only laterally a few setae; (1) with long and dense setae.
21. Dorsal posterior margin of metafemur: (0) smooth; (1) serrate.
22. Ventral posterior margin of metafemur in apical half: (0) smooth (at most minutely serrate in the apical quarter); (1) serrate.
23. Metatibia dorsally: (0) not carinate; (1) sharply carinate over all of its length; (2) carinate just in apical portion.
24. Metatibia, longitudinal carina on lateral face: (0) absent (Fig. 1P); (1) present on about two third of metatibial length (Fig. 1N); (2) present on basal third of metatibial length (Fig. 1O).

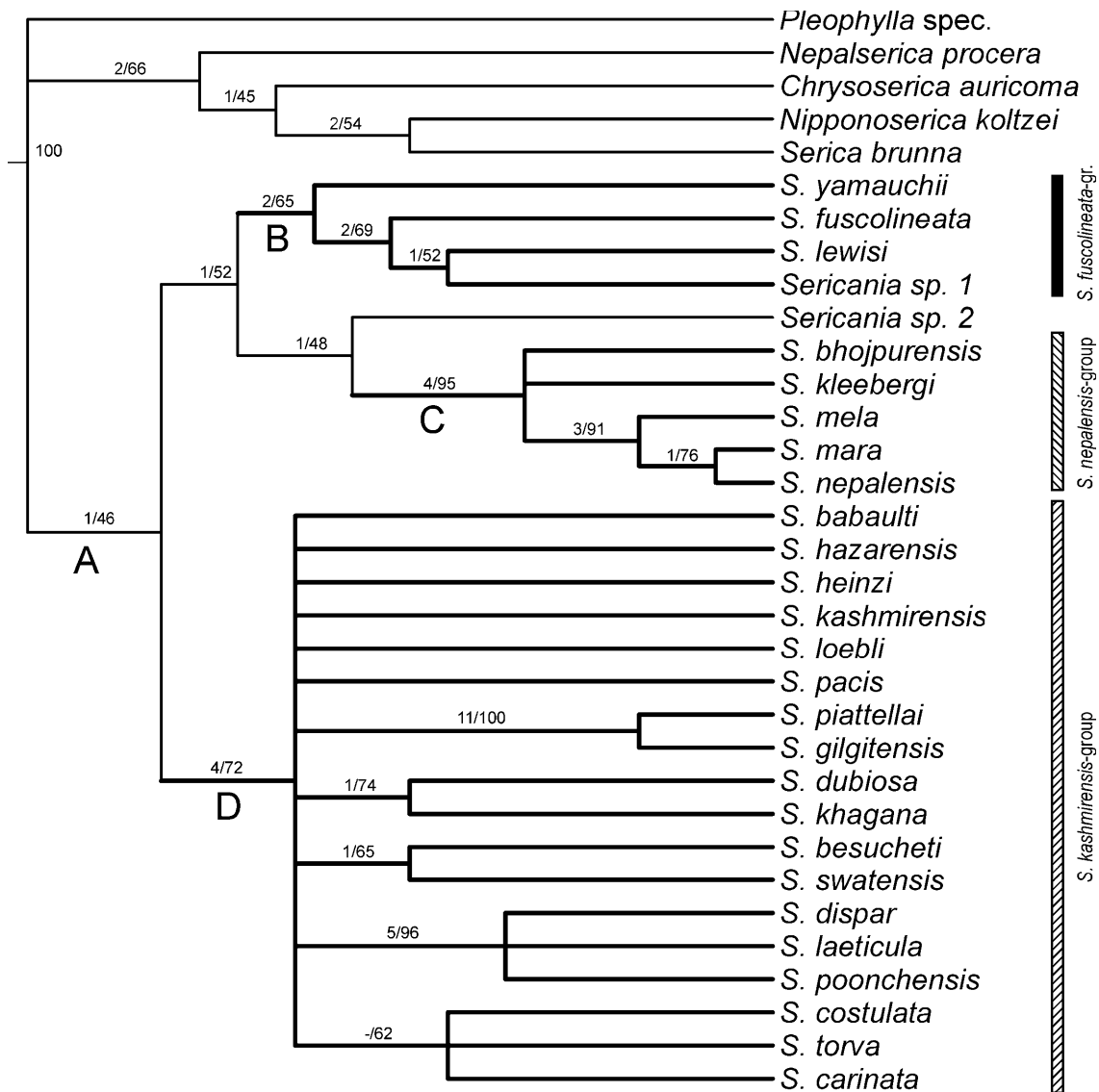


Fig. 3. Strict consensus (188 steps, CI: 0.39, RI: 0.67) of the 102 most parsimonious trees with a length of 171 steps (CI: 0.43, RI: 0.72); above each branch support indices (Bremer support/ Bootstrap values). *S.* = *Sericania*.

25. Metatibia, apex interiorly close to tarsal articulation: (0) bluntly angled, weakly concavely sinuate (Fig. 1S); (1) moderately truncate (Fig. 1Q); (2) sharply incised and strongly truncate (Fig. 1R).
26. Interior spines on apical face of metatibia: (0) present; (1) absent.
27. Tarsi dorsally: (0) smooth (Fig. 1S–U); (1) punctate.
28. Basal metatarsomere: (0) longer than the subsequent tarsomere (Fig. 1S, U); (1) as long as the subsequent tarsomere (Fig. 1T).
29. Metatarsomeres, subventral longitudinal carina beside serrate ventral ridge: (0) present (Fig. 1V); (1) absent (Fig. 1U).
30. Basal tooth of tarsal claws apically: (0) all sharply pointed; (1) all bluntly truncate; (2) claws of anterior tarsomeres bluntly truncate.

Male genitalia

31. Aedeagus, phallobase: (0) symmetrical (Fig. 2A–C, N–P); (1) asymmetrical (Fig. 2Q–Bb).
32. Aedeagus, apex of phallobase ventrally: (0) not produced into a ventrolateral lobe (Fig. 2E–G); (1) produced into a ventrolateral lobe (Fig. 2D, arrow).
33. Aedeagus, lateral sinuation before insertion of parameres ventrally: (0) moderately deep (Fig. 2A, C, F, G); (1) very deep, almost half of length of phallobase (Fig. 2K, M).
34. Aedeagus, phallobase ventroapically: (0) not produced into two ventromedian carinae (Fig. 2A, B, E); (1) produced into two ventromedian carinae (Fig. 2C, right arrow).
35. Ventral carina of phallobase: (0) weakly elevate (Fig. 2D, G, J); (1) strongly elevate (more than half as high as dorsoventral extension of phallobase at this position) (Fig. 2F, lower arrow).
36. Aedeagus, apex of phallobase (lateral view): (0) straight to weakly curved ventrally (Fig. 2D–G, J, K); (1) in apical third strongly curved ventrally (Fig. 2L, M).
37. Sclerotized portion of ventral phallobase apically: (0) deeply and narrowly sinuate (Fig. 2B); (1) convexly produced medially (Fig. 2A, C).
38. Aedeagus, phallobase dorsally: (0) longitudinally convex (Fig. 2N–P, R–Bb); (1) with a median longitudinal keel (Fig. 2Q).

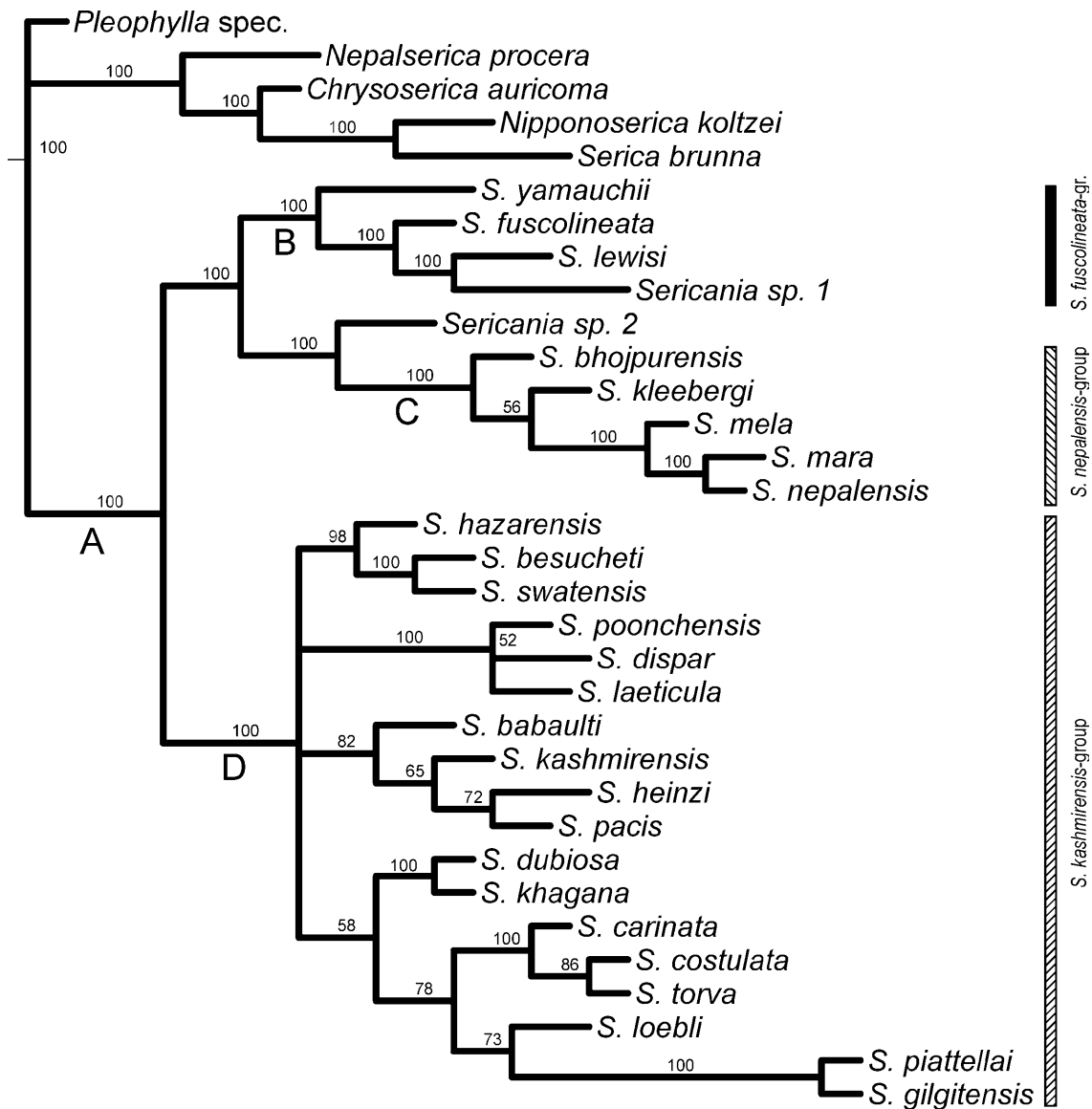


Fig. 4. Majority rule consensus (172 steps, CI: 0.43, RI: 0.71) of the 102 equally parsimonious trees (171 steps) resulting from parsimony ratchet based on equally weighted characters; above each branch is given the frequency (%) of a node among all MPT's. *S.* = *Sericania*.

39. Aedeagus, phallobase dorsally (lateral view): (0) evenly curved or plain (Fig. 2D–G, J, M); (1) distinctly impressed (Fig. 2K, L, left arrow).
40. Aedeagus, dorsal impression of phallobase (lateral view): (0) at middle (Fig. 2K); (1) at basal third (Fig. 2L).
41. Insertion of right paramere: (0) at the same level as the left (Fig. 2A–C); (1) more distal than the left paramere (Fig. 2X, Y); (2) more basal than the left paramere (Fig. 2W).
42. Parameres: (0) symmetrical (Fig. 2B, O, P); (1) asymmetrical (Fig. 2Q–Bb).
43. Parameres laterally: (0) longitudinally convex (Fig. 2D, E, K–M); (1) with a lateral keel, which is strongly produced and dorsoventrally flattened (Fig. 2F, G, arrow).
44. Parameres along all of its length: (0) straight (Fig. 2N, O, Q); (1) weakly curved inward (Fig. 2R, S); (2) strongly curved inward (Fig. 2P, T); (3) left paramere bent inward (Fig. 2W, Y).
45. Left paramere, basal lobe: (0) absent (Fig. 2N); (1) present (Fig. 2O–Bb).
46. Left paramere, basal lobe: (0) slender and long (longer than wide) (Fig. 2O); (1) large, circular; (2) very short (mostly covered by basal lobe of right paramere) (Fig. 2Q–T).
47. Left paramere, basal lobe: (0) produced basally and hooked at apex (Fig. 2U, Aa, Bb); (1) immediately produced basally, not hooked; (2) produced basomedially (Fig. 2W–Y); (3) produced basally and distally (Fig. 2P).
48. Left paramere, basal lobe: (0) comprising basal quarter of paramere (Fig. 2P, X); (1) comprising about basal third or more of paramere (Fig. 2W–Bb).
49. Right paramere, basal lobe: (0) absent (Fig. 2N); (1) present (Fig. 2O–Bb).
50. Right paramere, basal lobe: (0) short, at maximum half as long as distal portion of paramere (Fig. 2P, Q, S, T, W–Bb); (1) long, almost as long as distal portion of paramere (Fig. 2O, R, U).
51. Right paramere, basal lobe: (0) convexly rounded at apex (Fig. 2Q, T–Bb); (1) sharply pointed at apex (Fig. 2O, P, R, S).

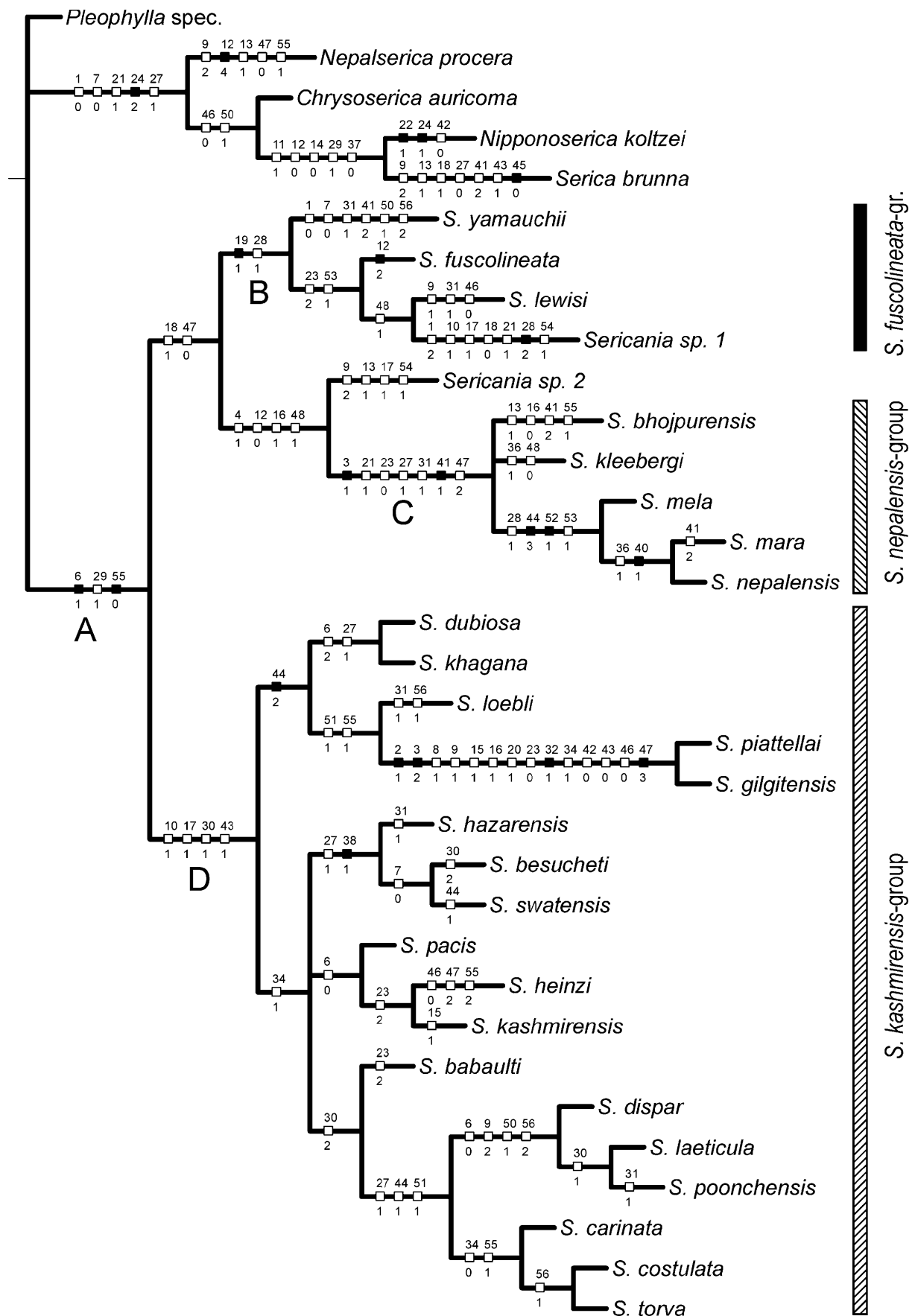


Fig. 6. Strict consensus (173 steps) tree of six MPTs (172 steps) resulting from successive approximation based on consistency index showing apomorphies mapped by state (discontinuous characters are mapped as homoplasy, DELTRAN optimization, unsupported nodes collapsed and using proportional branch lengths) (full squares – non-homoplasious character states; empty squares – homoplasious character states). *S.* = *Sericania*.

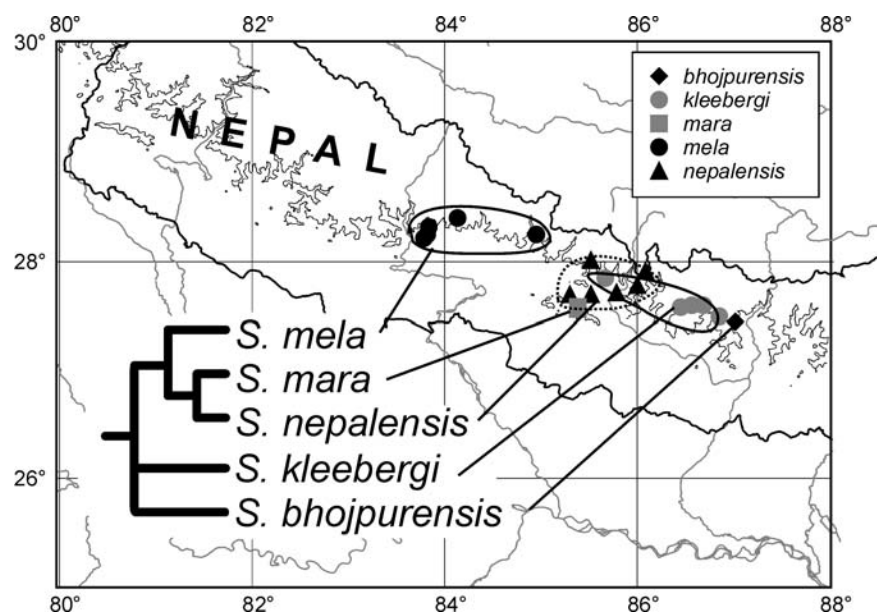


Fig. 7. Phylogeny of the *Sericania nepalensis* group in its geographical framework, with indicated distribution of the species, and 2000 meter altitude line. *S.* = *Sericania*.

port for the node *Sericania* is relatively low (node A: Bremer support: 1, bootstrap value: 46%). The information in the high number of equally parsimonious trees that resulted from the parsimony ratchet with equally weighted characters, is summarized by the majority rule consensus tree (Fig. 4).

The use of successive approximations character weighting (SACW, Farris, 1969) based on consistency index greatly reduced the number of most parsimonious trees (MPTs), producing a significantly more resolved strict consensus tree, especially among the representatives of the *Serica kashmirensis* group. In this approach weights no longer changed after two iterations. Six MPTs of 172 steps (CI: 0.55, RI: 0.78) resulted from the analysis, whose strict consensus tree was one step longer (Fig. 5). Although numerous nodes are well supported, especially those of the species groups indicated by the analysis with unweighted characters (Fig. 3, nodes B, C, D), the bootstrap values (calculated using character weights) for the several basal and apical nodes are low even after SACW.

DISCUSSION

Characters and computer analysis

The overall structure of the equally weighted majority rule consensus tree (Fig. 4) is the same as that indicated by the SACW analyses (Fig. 5), with one separate clade including *Nepaloserica*, *Chrysoserica*, *Nipponoserica* and *Serica*, and a second comprising all species of *Sericania*. Only in the latter clade is the topology altered slightly. The evolution of characters and evolutionary diversification of *Sericania* are discussed using the SACW strict consensus tree. Figure 6 illustrates the character changes along each branch under deltran optimization.

Characters of external morphology are consistent with the tree topology of the similar analyses based on male

genital characters, showing both similar consistency index (ci) and retention index (ri) means.

Monophyly of *Sericania*

Although not exhaustive, this study is the most comprehensive phylogenetic analysis of *Sericania* ever conducted. Due to the little variability in the genital features (Nomura, 1976), many of the Far East species of *Sericania* were not included in the cladistic analyses. All of them, however, share the same apomorphic states at node B as the taxa included. The results improve the current understanding of the relationships among the Asian Sericini.

The genus *Sericania* established by Motschulsky (1860) for a single species, *S. fuscolineata*, was comprised until recently only East Asian species, mainly from the Japanese Archipelago (Medvedev, 1952; Nomura, 1976). However, some of these species were reported recently from northern China, and moreover, taxa from the Himalaya were also assigned to this genus (Ahrens, 2004).

Monophyly of *Sericania* (node A), including the recently included new taxa from the Himalaya, is evident from both analyses with unweighted and weighted characters (Figs 3, 5, node A). It is supported by a number of unambiguous apomorphies: (1) surface of labroclypeus convexly elevate medially (6 : 1); (2) subventral longitudinal carina beside serrate ventral ridge of metatarsomeres absent (29 : 1); and (3) right paramere with a basal lobe directed medially (55 : 0).

The search for the sister taxon of *Sericania*, using the tree topology of the present analyses was unsuccessful. This might be a consequence of our poor knowledge of the Asian sericine fauna. But it is also evident from other similar studies (Ahrens, 2006 and unpubl. results), that the morphological characters of Sericini are only little suitable to resolve basal nodes of major species groups or

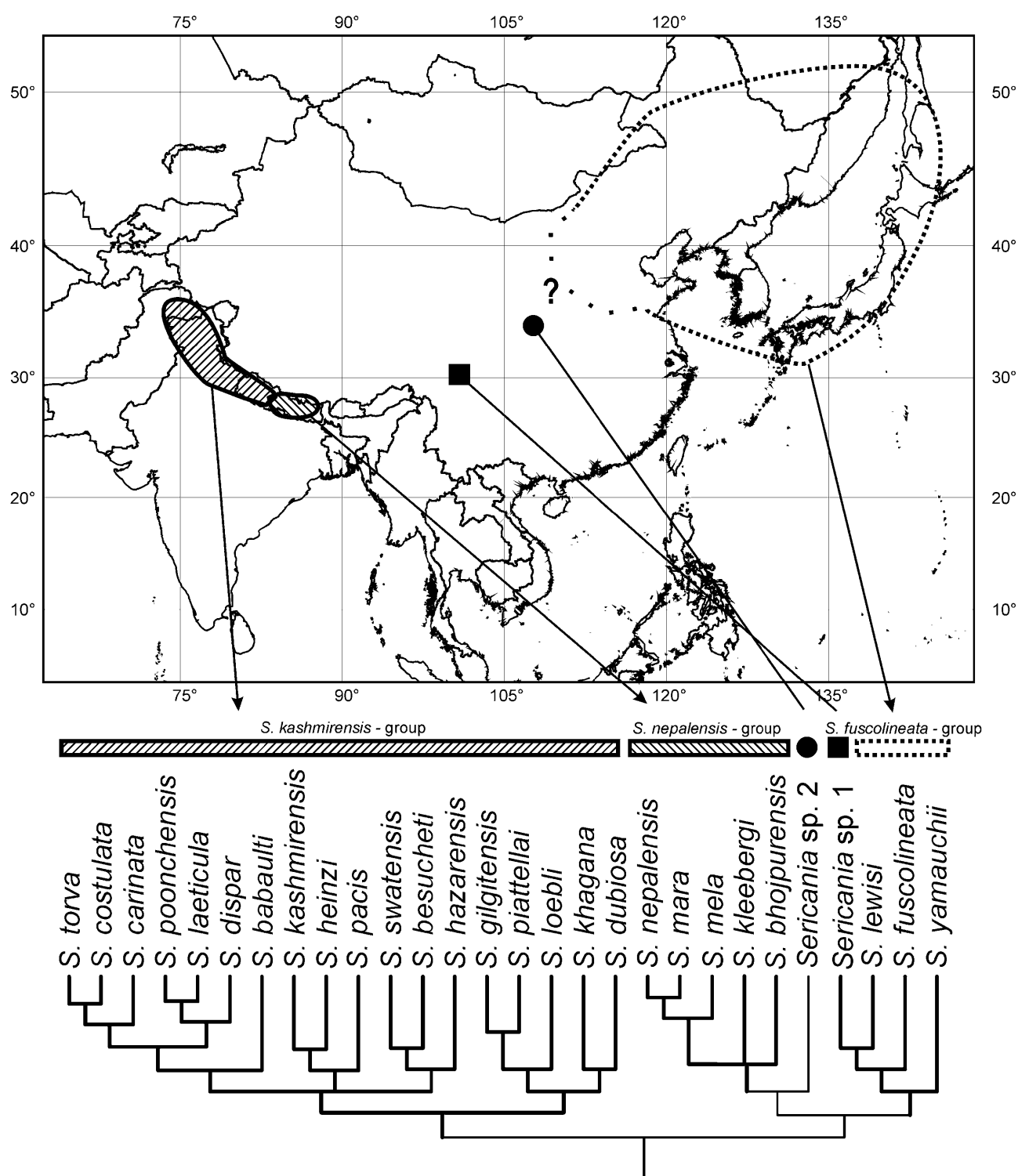


Fig. 8. Phylogeny of *Sericania* in its geographical framework. Cumulative generalized distribution of the principal lineages (with bold tree branch lines) is shown, with the respective ranges indicated as follows: *S. kashmirensis*-group – continuous line and shaded from right to left; *S. nepalensis*-group – continuous line and shaded from left to right; *S. fuscolineata*-group – dotted line. *S.* = *Sericania*.

genera due to the high number of taxa (~ 200 genera of Sericini presently described from Palaeotropical region; Ahrens unpublished data) and a limited number of available informative characters.

Evaluation of the clades and evolution of *Sericania*

Among the three major lineages recognized from both strict consensus trees (Figs 3, 5) the *Sericania fuscolineata* group represents the genus *Sericania* as defined “originally” by Motschulsky (1860) and adopted by subsequent authors (e.g. Medvedev, 1952; Nomura, 1976).

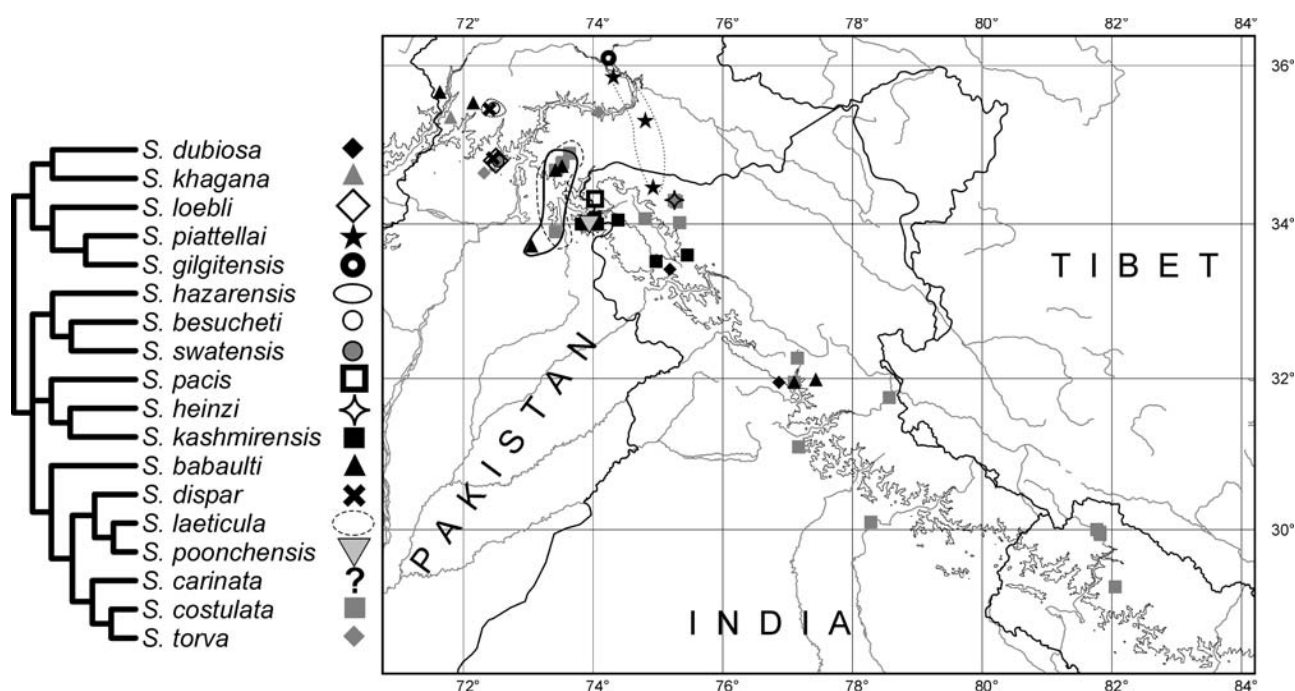


Fig. 9. Phylogeny of the *Sericania kashmirensis* group in its geographical framework, with indication of the distribution of the species and 2000 meter altitude line. *S.* = *Sericania*.

Its monophyly is best supported by the following apomorphies (see node B, Fig. 6): (1) metacoxa transversely impressed (19 : 1); and (2) basal metatarsomere as long as the subsequent tarsomere (28 : 1). The species of this clade are so far only reported from the Far East Asia, but a still undescribed taxon (*Sericania* sp. 1) is reported here also from the eastern margin of the Tibetan Plateau. This species is nested in a node among the representatives of this group.

The sister taxon relationship of the *Sericania fuscolineata* group with the second major clade of *Sericania*, the *Sericania nepalensis* group + *Sericania* sp. 2, is based upon (1) the scutellum compared to elytral base narrow (18 : 1); and, as apparent under DELTRAN and ACC-TRAN optimization (Fig. 6), (2) the metatibia at apex interiorly close to tarsal articulation sharply incised and strongly truncate (25 : 2). The male genitalia of *Sericania* sp. 2 from Shaanxi (China) have in several apomorphies that differ notably from the basic pattern of the *Sericania fuscolineata* and *Sericania nepalensis* groups, which is reflected in the little support for the branch of *Sericania nepalensis* group + *Sericania* sp. 2. Consequently, I prefer not to assign *Sericania* sp. 2 to the formally established and well supported *Sericania nepalensis* group (node C). The areas, where *Sericania* sp. 1 and sp. 2 occur, are still poorly investigated, and additional representatives of further lineages are likely to be discovered. The representatives of the *Sericania nepalensis* group are restricted to the central Himalaya, where they diversified little compared to other groups endemic to the Himalaya (Fig. 7).

According to the phylogeny indicated by this cladistic analysis, the Himalayan *Sericania* species are not a monophyletic group, but two separate lineages. The *S.*

nepalensis clade, is nested within a clade composed in major part of East Asian species (Fig. 8), and which is sister taxon to the second Himalayan clade, the *Sericania kashmirensis* group. This reveals that faunal exchange must have occurred at least twice, but fossils and a better knowledge of the Chinese sericine fauna are needed to determine the direction.

The *Sericania kashmirensis* group species are mainly restricted to the Indus Himalaya (Troll, 1972). A few further east. Ranges of many of its taxa are based on a fragmentary exploration of the areas which results in widely isolated occurrences (Fig. 9), such as in *S. babaulti*, *S. laeticula*, and *S. hazarensis*. In several cases closely related species (sister taxa) occur sympatrically (Fig. 9), such as *S. laeticula* and *S. poonchensis*, or are close neighbours, as in *S. gilgitensis* and *S. piattellai*, *S. heinzi* and *S. kashmirensis*, *S. costulata* and *S. torva*, and *S. besucheti* and *S. swatensis*. There are no endemic forms east of the Indus Himalaya. The Indus Himalaya there is an arboreal belt, unlike in all other regions of the Himalaya, which is delimited at high altitude by the alpine vegetational belt, and at lower altitude (below ~ 2000 m) by desert steppe (Troll, 1972; Fig. 10). Most of the species of Sericini dwell in arboreal habitats (Ahrens, 2004) and avoid the alpine belt. This upper and lower altitudinal vegetational delimitation is supposed to be important for survival during periods of climatic deterioration, or dispersal to adjoining areas. This might explain, why species adapted to aridity are restricted to the north-western Himalaya and found not in drier regions of the Tibetan Highlands or inner valleys of the central Himalaya, and why closely related species occur in neighbouring areas. However, in extremely arid habitats the pressure of com-

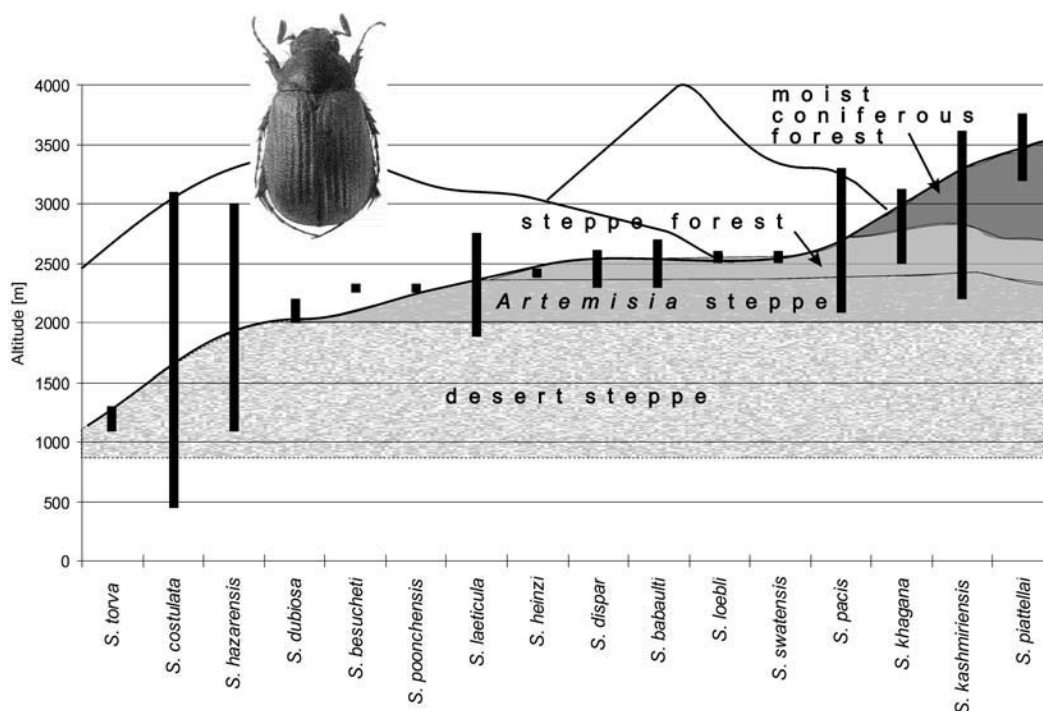


Fig. 10. Altitudinal distribution of the taxa of the *Sericania kashmirensis* clade (*S. gilgitensis* omitted due to lack of data) in the context of the climatic and vegetational zonation of the Indus Himalaya (according to Troll, 1972) where the vast majority of the species of the *Sericania* occur. *S.* = *Sericania*.

petition from hygrophilous eastern elements of Himalayan sericine fauna is absent.

Interiors of large continents are normally arid because of their great distance from sources of ocean moisture, but sediments deposited in the western Loess plateau of East Asia indicate these areas were fluvial-lacustrine during the Oligocene epoch (Wang, 1985) and had a more humid climate. One source of moisture during the Oligocene in the Asian interior may have been the Paratethys sea in western Central Asia (Ramstein et al., 1997). As this inland sea shrank during the late Oligocene and early Miocene, the Asian interior have become more arid and the climate more continental, with hotter summers and colder winters. The onset of greater aridity recorded by the early Miocene loess (Guo et al., 2002) in the Qinan deposits in northern China (Gansu province) is broadly consistent with this change in land-sea distribution. These Qinan deposits indicate that by the early Miocene the winter wind pattern was similar to the modern Asian winter monsoon.

Based on the present distribution of the *Sericania kashmirensis* clade in the drier parts of the North-West Himalaya it is hypothesized that the stem species of this clade was also xerophilous and less adapted to the humid conditions, which today prevail on the southern slopes of the central and eastern Himalaya. Provided that the stem species (Fig. 6, node D) of the *S. kashmirensis* clade was xerophilous, this clade will not predate the early Miocene. One conceivable hypothesis is that the extension of distribution of the species of the *S. kashmirensis* clade was former wider along the northern margin of the rising Tibet, which possibly achieved a high elevation much

later (Pliocene to Quaternary) than the southern margin (Tapponier et al., 2001), which reached considerable elevation already in the Eocene/Oligocene. The climatic and altitudinal divide along the Tertiary orogenic belt (southern Tibet, Himalaya) might have been an effective barrier separating the two basal lineages of *Sericania*. The highest elevation could have been achieved by early Miocene, since fossil plant 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). The present range of the *S. kashmirensis* clade would constitute just a relic of a formerly more extensive northern distribution.

On the other hand, the occurrence of taxa of the sister lineage of the *S. kashmirensis* clade (*S. nepalensis* group) on the southern slopes of the Himalaya, indicate that the separation of the basal *Sericania* lineages may have occurred along the southern slope of the Himalaya/Tibet and probably coincided with the onset of monsoons around 8 Ma (Prell et al., 1992, Quade et al., 1989). The east-west contrast in climate along the southern slope of the Himalaya have strengthened significantly since that time (Ramstein et al., 1997, Ruddiman & Kutzbach, 1989; Manabe & Broccoli, 1990; An et al., 2001).

Considering the stem lineage taxa of *Sericania* more hygrophilous, the sister taxon to the *S. kashmirensis* clade probably evolved close to the south-eastern margin of the present Tibetan Highlands and the stem lineage of the *S. nepalensis* group possibly dispersed westwards along the southern Himalayan slope, and the ancestral taxa of the *S. fuscolineata* group moved to the north-east. The latter have strongly diversified on the Japanese Archipelago.

The preliminary results and discussions presented here are part of a wider study of the sericine beetle component of the fauna of the Tertiary orogenic belt. Further exploration of the Asian Fauna of Sericini, the discovery of new taxa and the identification of the sister taxon of *Sericania* (in further phylogenetic studies) will help to determine the origin of the stem species of *Sericania* and, in particular, provide evidence for one of the two hypotheses for the evolution of the xerophilous *S. kashmirensis* lineage.

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