

3.2.6 The phylogeny of *Xenosericica* gen. n.

The Himalayan Sericine chafers have been revised extensively using almost all collection material available to the author (Ahrens 1995a – 2004c; Ahrens and Sabatinelli 1996). These studies, recently concluded and summarized by Ahrens (2004b), revealed that flight reduction did apparently not occur among Himalayan Sericini. This peculiarity, in contrast to many other Himalayan Coleoptera (Carabidae, Chrysomelidae) with numerous apterous or brachypterous forms (Mani 1968), was explained by the absence of Sericini in the alpine and nival zone. Recently, however, brachypterous individuals were collected in the alpine zone of the slopes of the Kali Gandaki Valley (Fig. 83).

Material and methods

Taxon sampling and characters

Nineteen species belonging to eight genera of Sericini were included in the cladistic analysis, with *Comaserica bergrothi* chosen as the outgroup taxon due to their rather close relationship to the ingroup taxa, but with a high probability of not being part of the ingroup (chapter 3.1). Character coding was based on 22 species belonging to nine genera (see appendix A 3.2.6). The choice of taxa to be included into the ingroup was mainly based on present and historical classification of the species and genera of Sericini (e.g. Nomura 1976, Yu et al. 1998). Representatives of the Central Asian endemic genus *Trochaloschema* were also included because they represent the only previously known Asian sericine chafers having reduced wings. Thirty-six adult characters were scored. The character states are illustrated in Figs 84-86. Characters resulting directly from brachyptery were not considered in the analyses to exclude the possibility that environmentally driven adaptations (wing reduction, with a high probability of convergence could influence the results of the analysis.

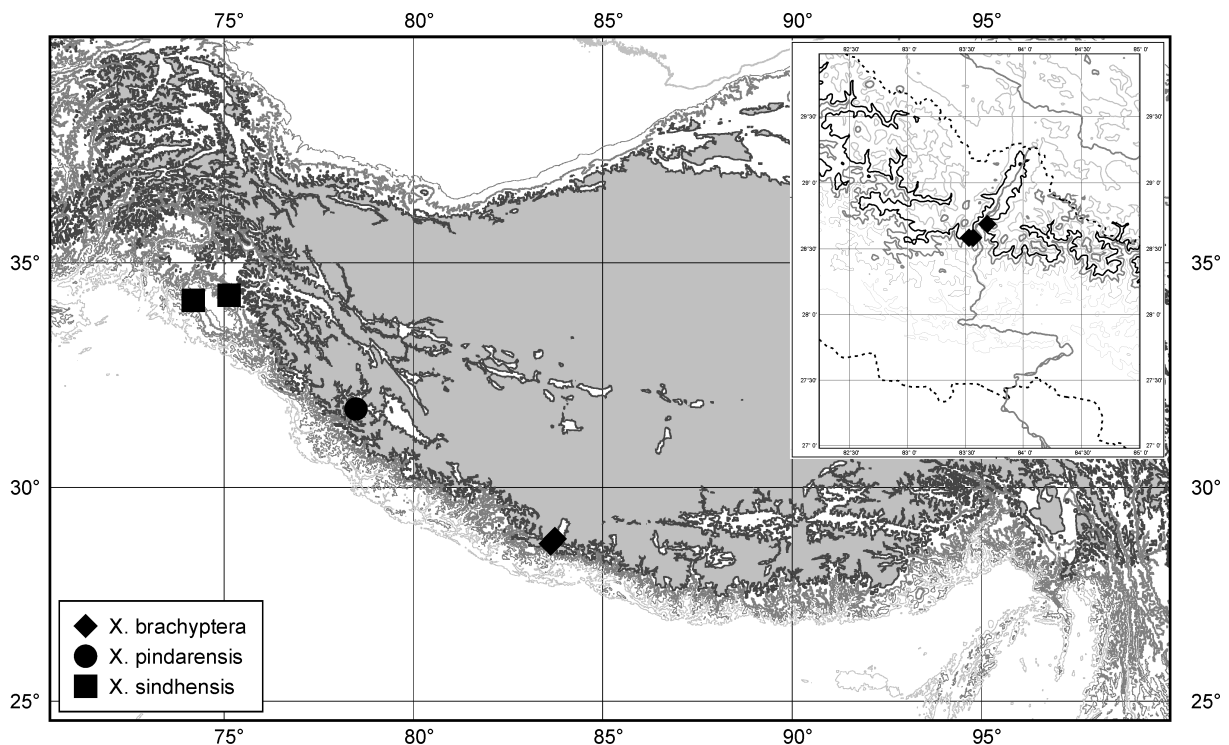


Fig. 83. Distribution of the new genus *Xenosericica* endemic in the Himalaya, including a more detailed map with the records of the only brachypterous sericine chafer of the Himalaya, *Xenosericica brachyptera* sp. n.

Phylogenetic analysis

The 36 characters (27 binary and 9 multistate) were all unordered and equally weighted. Inapplicable characters were coded as „-“, while unknown character states were coded 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 three. 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.

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, 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.

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. In addition to the character description, the consistency index (ci) and the retention index (ri) calculated by via WINCLADA are given. The data matrix is presented in appendix B 3.2.6.

Integument

1. *Surface of the body*: (0) with dull cover of microtrichomes; (1) shiny, without dull cover of microtrichomes (Fig. 84A) (ci: 0.33, ri: 0.66).

Head

2. *Anterior margin of labroclypeus medially*: (0) distinctly sinuate (Fig. 84H); (1) very shallowly sinuate (Fig. 84J) (ci: 0.25, ri: 0.25).
3. *Eyes in male*: (0) medium sized, ratio of diameter/ interocular width ~ 0.7-0.5 (Fig. 84H); (1) small, ratio of diameter/ interocular width < 0.5 (Fig. 84A); (2) very large, ratio of diameter/ interocular width ~ 0.8 (Fig. 84N) (ci: 0.4, ri: 0.4).
4. *Total number of antennomeres*: (0) ten; (1) nine (ci: 0.5, ri: 0.83).
5. *Number of antennomeres of clavus in male*: (0) three (Fig. 84L); (1) four (Fig. 84N); (2) seven (Fig. 84M) (ci: 1.0, ri: 1.0).
6. *Number of antennomeres of clavus in female*: (0) three; (1) four; (2) five (ci: 1.0, ri: 1.0).

Thorax

7. *Prothorax, hypomeron ventrally*: (0) not carinate; (1) carinate (ci: 0.5, ri: 0.66) (chapter 3.1).
8. *Mesosternum between mesocoxae*: (0) narrow (narrower than mesofemur medially) (Fig. 85B); (1) wide (wider than mesofemur medially) (Fig. 85A) (ci: 0.5, ri: 0.66).
9. *Mesofurca and mesosternum, carina from craniolateral margin of mesosternum to mesofurcal arm*: (0) absent; (1) present (Fig. 85C) (ci: 1.0, ri: 1.0) (chapter 3.1).

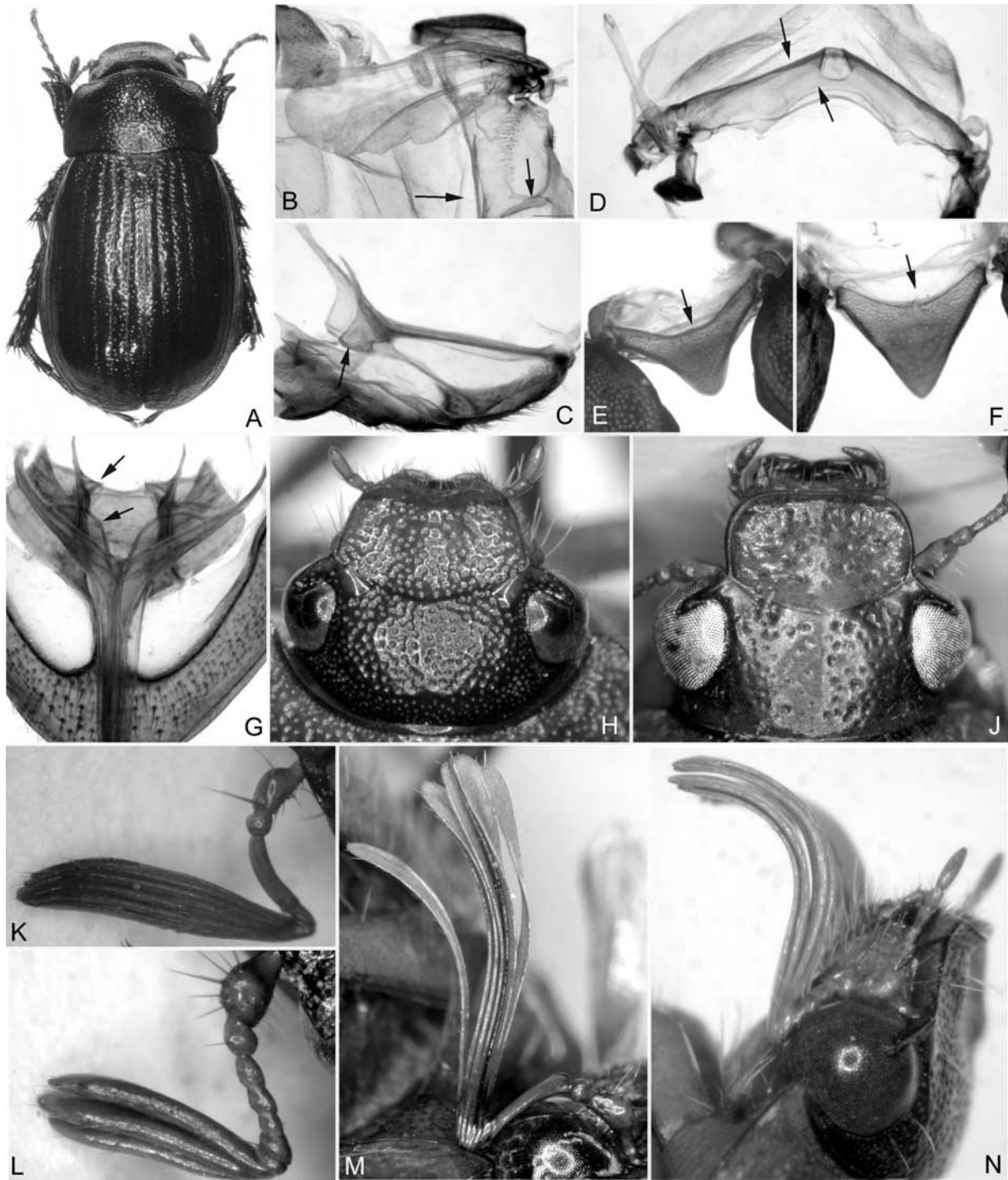


Fig. 84. A-C, F, G, L: *Xenoserica brachyptera*; D, E: *Trochaloschema* sp.; H, N: *Pseudosericania quadrifoliata*; J: *Gastroserica asulcata*; K: *Pleophylla* sp.; M: *Nepaloserica procera*. A: habitus; B: ala and metanotum, with postnotum completely reduced (arrow); C: metafemur, lateral view; G: meso- and metafemur, dorsal view; H, J: head, dorsal view; K-N: antenna of male (not to scale).

Legs

10. *Long setae on ventral face of metacoxa*: (0) laterally only (Fig. 85D); (1) on entire surface (Fig. 85E) (ci: 1.0, ri: 1.0).
11. *Ventral posterior margin of metafemur in apical half*: (0) smooth (at most in the apical quarter minutely serrate) (Fig. 85G); (1) serrate (Fig. 85F) (ci: 1.0, ri: 1.0).
12. *Dorsal posterior margin of metafemur*: (0) smooth; (1) serrate (ci: 0.5, ri: 0.66).
13. *Metatibia dorsally*: (0) not edged (Figs 85H,L); (1) sharply edged (Figs 85J,K,M,N) (ci: 1.0, ri: 1.0).

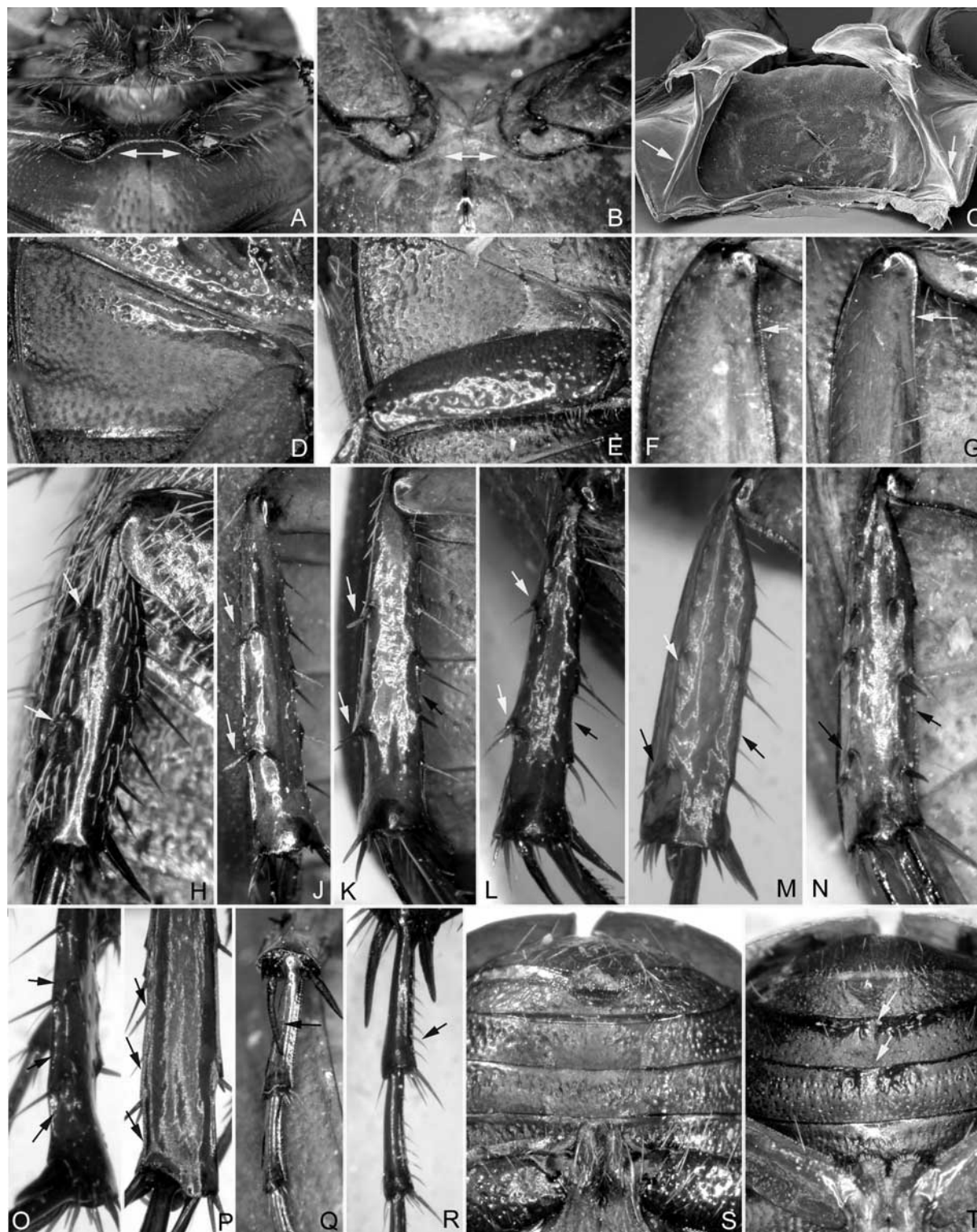


Fig. 85. **A:** *Maladera insanabilis*; **B, D, F, N, Q:** *Nipponoserica koltzei*; **C:** *M. holosericea*; **E, L, O, R, S:** *Xenoserica sindhensis*; **G, J, K, P:** *Nepaloserica procera*; **H:** *Pleophylla* sp.; **M:** *Pseudosericania quadrifoliata*; **T:** *N. sulciventris*. **A, B:** meso- and metasternum (ventral view); **C:** mesosternum with mesofurca bearing a cranio-lateral ridge; **D, E:** metacoxa, ventral view; **F, G:** distal portion of metafemur, ventral view; **H, K-N:** metatibia, lateral view; **J:** metatibia, dorsolateral view; **O:** metatibia, ventral view; **P:** metatibia, medial view; **Q, R:** metatarsomeres, lateral view; **S, T:** abdomen, ventral view (not to scale).

14. *Lateral face of metatibia (posterior half)*: (0) not carinate (Figs 85H,L); (1) acutely longitudinally carinate on dorsal portion of basal two thirds of length (Figs 85M,N); (2) convexly longitudinally carinate on lateral face in basal third of metatibial length (Figs 85J,K) (ci: 1.0, ri: 1.0).

15. *Number of groups of robust spines on dorsolateral face of metatibia*: (0) two (Figs 85H-L); (1) one (Figs 85M,N) (ci: 1.0, ri: 1.0).
16. *Ventral margin of metatibia*: (0) sharply carinate (Figs 85K,M,N,P); (1) longitudinally convex (Figs 85H,L,O) (ci: 1.0, ri: 1.0).
17. *Ventral margin of metatibia*: (0) serrate (Figs 85K,M,N,P); (1) not serrate (Figs 85H,L,O) (ci: 1.0, ri: 1.0).
18. *Carina on lateral face of metatibia*: (0) not serrate (Fig. 85N); (1) serrate (Fig. 85M) (ci: 1.0, ri: 1.0).
19. *Ventral posterior margin of mesofemur in apical half*: (0) smooth; (1) serrate (ci: 1.0, ri: 1.0).
20. *Metatarsomeres laterally*: (0) not carinate (Fig. 85R); (1) carinate (Fig. 85Q) (ci: 0.5, ri: 0.8).
21. *Metatarsomeres dorsally*: (0) smooth; (1) punctate; (2) with longitudinal impressions (ci: 0.5, ri: 0.6).
22. *Setae on ventral face of metatarsomeres 1-4*: (0) present (Fig. 85Q); (1) absent (Fig. 85R) (ci: 0.5, ri: 0.85).

Wings

23. *Apical margin of elytra*: (0) without short microtrichomes; (1) with short microtrichomes (ci: 0.33, ri: 0.5).
24. *Alae*: (0) fully developed; (1) brachypter (Figs 84B,D) (ci: 0.5, ri: 0.5).

Abdomen

25. *Penultimate abdominal sternite*: (0) not impressed medially (Fig. 85S); (1) longitudinally impressed medially (Fig. 85T) (ci: 1.0, ri: 1.0).

Aedeagus

26. *Phallobase*: (0) symmetrical (Figs 86A,C-L); (1) asymmetrical (Fig. 86B) (ci: 1.0, ri: 1.0).
27. *Apical phallobase laterally*: (0) not produced (Figs 86A-D,F-K,M,N,P,Q); (1) distinctly produced on each side of parameres (Figs 86E,L,O,R) (ci: 1.0, ri: 1.0).
28. *Dorsomedian sinuation of phallobase*: (0) one third as long as distal portion of phallobase (Figs 86D,F,G); (1) half as long as distal portion of phallobase (Figs 86F,L,R); (2) more than half as long as distal portion of phallobase (Figs 86K,Q) (ci: 0.4, ri: 0.57).
29. *Ventral face of phallobase medially*: (0) in distal half membranous (Fig. 86C); (1) in distal third membranous (Fig. 86A) (ci: 1.0, ri: 1.0).
30. *Parameres*: (0) symmetrical (Figs 86A,E-L); (1) asymmetrical (Figs 86B,D) (ci: 0.33, ri: 0.66).
31. *Apex of parameres*: (0) convexly rounded (Figs 86B,E,G,J); (1) widened (Figs 86K,L); (2) sharply pointed (Figs 86D,F,H) (ci: 0.66, ri: 0.66).
32. *Parameres apically*: (0) curved outward (Fig. 86J); (1) parallel and straight (Figs 86E,G,K,L); (2) convergent (Figs 86D,F,H) (ci: 0.66, ri: 0.8).
33. *Parameres basally both*: (0) not produced beyond insertion (Figs 86B,D,G); (1) produced (Figs 86E,F,H-L,M-R); (2) only right paramere produced (ci: 0.66, ri: 0.85).
34. *Basal process of parameres*: (0) not widened dorsoventrally (Figs 86M,N); (1) widened dorsoventrally (Fig. 86P) (ci: 1.0, ri: 1.0).
35. *Parameres medially*: (0) as high as wide (Figs 86C-E,G,J-L,N-R); (1) wider than high (dorsoventrally flattened) (Figs 86F,H,M) (ci: 1.0, ri: 1.0).
36. *Temonoes*: (0) distinctly longer than wide (Fig. 86T); (1) distinctly shorter than wide (Fig. 86S) (uninformative).

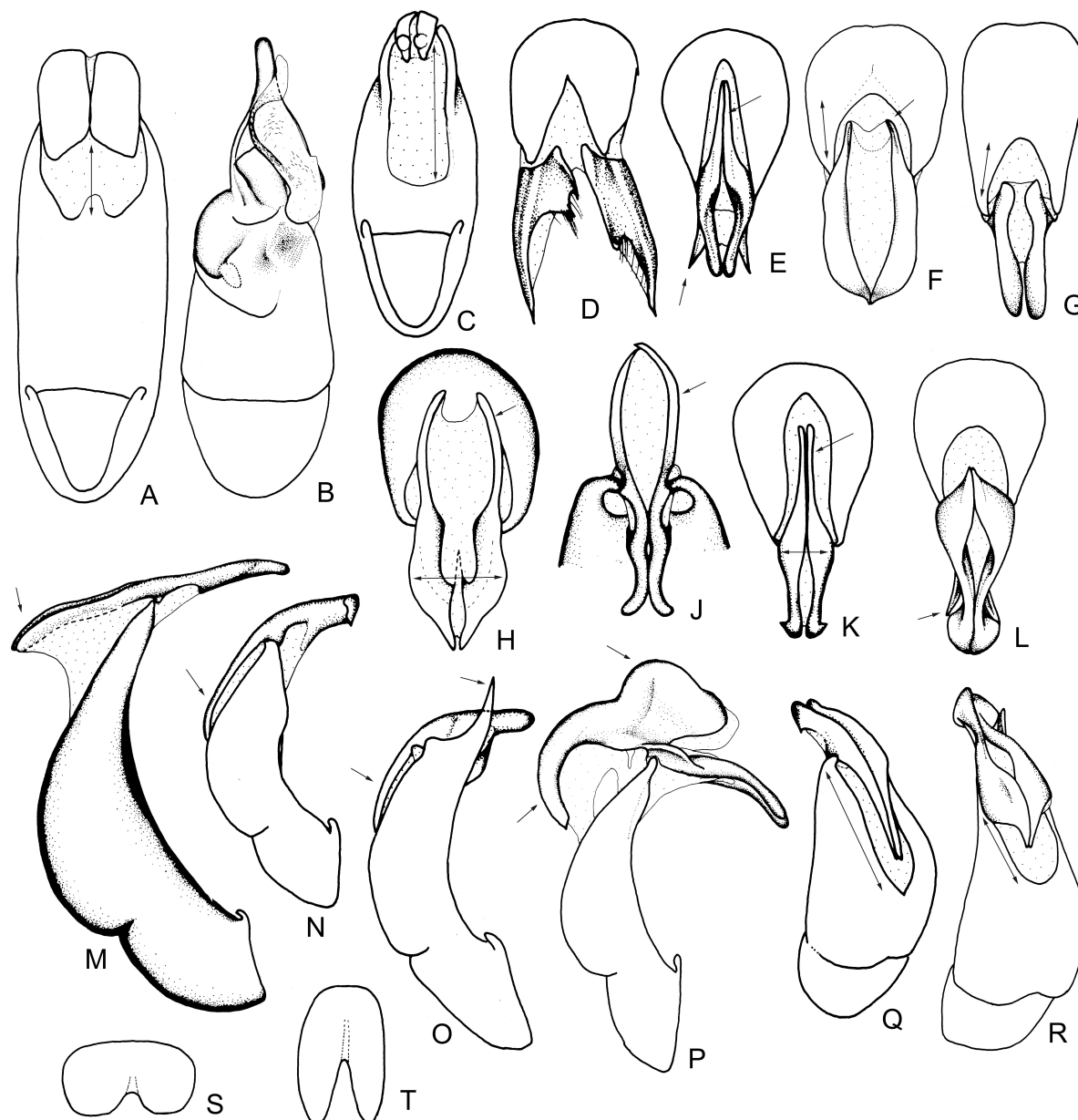


Fig. 86. A, F, S: *Xenosericia brachyptera*; B: *Maladera simlana*, C, K, N, Q, T: *Nipponoserica koltzei*; D: *Pleophylla* sp.; E, O: *N. pubiventris*; G: *Stilbolemma sericea*; H, M: *X. sindhensis*; J: *X. pindarensis*; L, R: *N. peregrina*; P: *Pseudosericania quadrifoliata*. A, B: meso- and metasternum (ventral view); C: mesosternum with mesofurca bearing a craniolateral ridge; D, E: metacoxa, ventral view; F, G: distal portion of metafemur, ventral view; H, K-N: metatibia, lateral view, J: metatibia, dorsolateral view; O: metatibia, ventral view; P: metatibia, medial view; Q, R: metatarsomeres, lateral view; S, T: abdomen, ventral view (not to scale).

Results

The analysis of 36 adult characters with the parsimony ratchet and the above mentioned settings yielded two equally parsimonious trees (Fig. 89) of 72 steps (CI: 0.62, RI: 0.82). Repeating the search ten times, I obtained the same statistics as above. Character 36 proved uninformative in the present data set. The strict consensus of these trees, with jackknife values and Bremer support, is presented in Fig. 87 as the preferred hypothesis of relationships between the taxa because it shows the areas of tree conflict as polytomies. 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 rather in an increasing number of equally parsimonious trees. The tree topology was not affected by altering ACCTRAN or DELTRAN optimization.

The strict consensus tree (Fig. 87) shows three major clades: (1) the genus *Trochaloschema*, which is endemic in the Pamir mountains, (2) *Xenosericia* gen. n., and (3) the remainder taxa of the ingroup including the representatives of the genera *Nepaloserica*, *Maladera*, *Stilbolemma*, *Nipponoserica*, and *Pseudosericania*. Based on the analysis, the latter two genera appear to form a single monophyletic group.

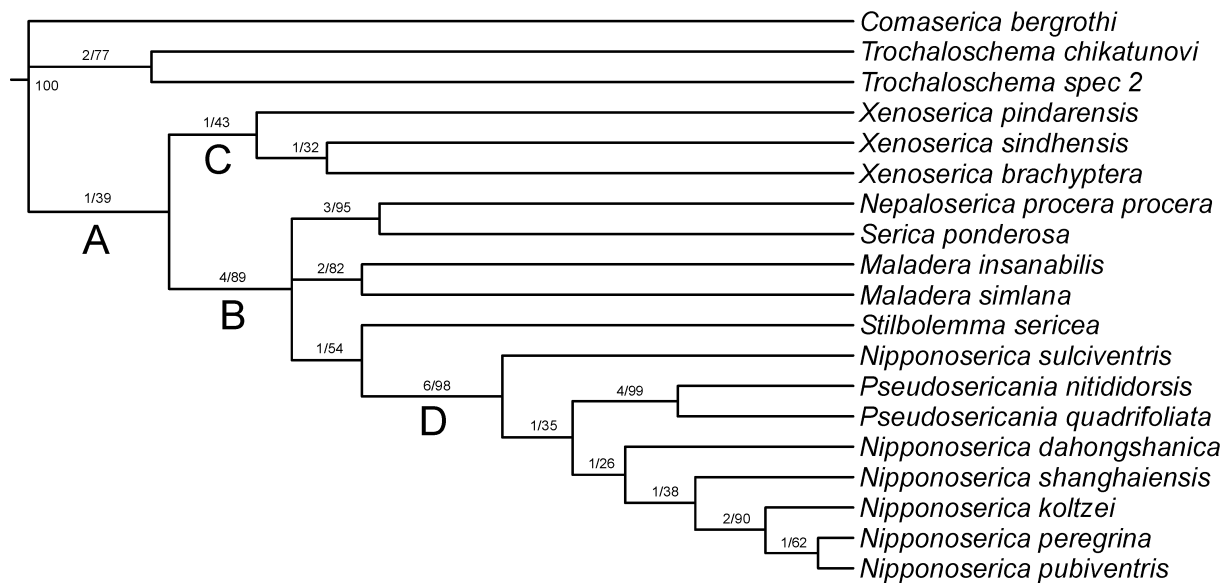


Fig. 87. Strict consensus of the two equally parsimonious trees with a length of 72 steps (CI: 0.62 and RI: 0.82); above each branch support indices (Bremer support/ jackknife values).

Discussion

The Himalayan *Xenosericia* species, formerly assigned to *Nipponoserica* (Ahrens 2000c) due to the uniquely formed parameres of male genitalia, are not closely related to *Nipponoserica*, but occupy a more basal position within the clade of ‘modern’ Sericini (represented herein by *Maladera*, *Nepaloserica*, *Nipponoserica*, *Pseudosericania*, and *Xenosericia*). The clade of ‘modern’ Sericini (node A) shares the following unambiguous apomorphic character states: (1) total number of antennomeres ten (4:0); (2) carina from cranio-lateral margin of mesosternum to mesofurcal arm present (9:1); (3) the dorsal posterior margin of metafemur serrate (12:1); and (4) apical margin of elytra with short microtrichomes (23:1). A parallel analysis considering the wing venation provides, additionally, a further apomorphy (anterior anal vein (AA) acutely bent; chapter 3.1) for that node, but this has no impact here since characters affected by wing reduction were not included in the present analysis.

One of the principal clades (node B) of these ‘modern’ Sericini included in the matrix is rather well supported (Bremer support: 4, jackknife value: 89 %) by several unambiguous apomorphies: (1) metatibia dorsally sharply edged (13:1); (2) ventral margin of metatibia sharply carinate (16:0) and (3) serrate (17:0); (4) parameres asymmetrical (30:1); and (5) parameres apically parallel and straight (32:1). The sister group to this clade is *Xenosericia* (node C). As far as is known, the latter is endemic to the Himalaya. One species (*X. brachyptera* sp. n.) has wings reduced in length in both sexes (Fig. 84C), a condition previously unknown among Himalayan phytophagous Scarabaeidae. With respect to wing reduction, this species particularly resembles other brachypterous groups such as

Trochaloschema. However, as indicated by the cladogram, these are solely convergences caused by similar pressures, such as arid high altitude conditions. The following unambiguous apomorphies were identified for this clade (node C): (1) long setae on ventral face of metacoxa on entire surface (10:1); (2) dorsomedian situation of phallobase half as long as distal portion of phallobase (28:2); (3) parameres basally both distinctly produced beyond the insertion (33:1). Interestingly, neither the geographically proximate species (*X. sindhensis*/*X. pindarensis* or *X. brachyptera*/*X. pindarensis*, Fig. 83), nor the two fully winged species (*X. sindhensis*/*X. pindarensis*) (being in habitus much more similar) are more closely related, but geographically separated *X. sindhensis* and *X. brachyptera* share the sharply pointed apex of parameres (32:2) and the medially dorsoventrally flattened parameres (35:1). The occurrence of all three species in the Himalaya seems to be a relic since the ranges of the three species are widely separated from one another.

The genus *Nipponoserica* is positioned within the monophyletic clade B (node D, Bremer support: 6, jackknife value: 98 %), along with representatives of the genus *Pseudosericania*. The latter is a monophyletic Taiwanese lineage (Bremer support: 4, jackknife value: 99 %) nested within the clade of taxa presently classified as *Nipponoserica*. Its four species presently known (*P. gibbiventris*, *P. makiharai*, *P. nitididorsis* and *P. quadrifoliata*) share a number of apomorphies (see Fig. 6: 3:2, 5:1, 18:1, 34:1). Based on the examination of additional specimens and of the original descriptions (Nomura 1976, Sawada 1937, Chapin 1938), the clade *N. pubiventris* + *N. peregrina* should to contain all Japanese taxa of *Nipponoserica*: *N. daisensis daisensis* (Sawada, 1937), *N. daisensis lewisi* (Chapin, 1938), *N. gomandana* Nomura, 1976, *N. kunitachiana* Nomura, 1976, *N. setiventris* Nomura, 1976, *N. similis* (Lewis, 1895). *N. laferi* (Nikolaev, 1980), which could be evaluated only through reading the original description (Nikolaev 1980), should belong to the *N. koltzei* (*N. pubiventris*, *N. peregrina*) lineage. Unfortunately, I had no specimens of the remaining taxa [*N. babai* Kobayashi, 1991, *N. takeuchii* Hirasawa, 1991, and *N. elliptica* (Murayama, 1938)] to include in this analysis.

Trochaloschema, included in the ingroup, does not share any apomorphies with the remaining ingroup taxa. Consequently, its relationship to the other taxa included into this analysis remains obscure. However, members of this genus possess a number of unambiguous homoplasious apomorphies (3:1, 8:1, 24:1), of which some were not considered in this study since they are evidently autapomorphies within the genus (e.g. the short scutellum as an adaptation to flight reduction, see Fig. 84E, or the lateral rudimentary basal pronotal margin).

Considerations for classification

Since this is a preliminary analysis of phylogenetic relationships among sericine chafers, conclusions related to classification in general should be drawn with caution to maintain nomenclatural stability at a reasonable level.

Based on tree topology (Figs 5, 6), the most apparent question is, whether to regard *Pseudosericania* Kobayashi, 1980 as a subjective synonym of *Nipponoserica* Nomura, 1972, the first nested within the species presently considered as *Nipponoserica*. Although *Pseudosericania* is based on a number of good apomorphies, the clade (*Nipponoserica sulciventris* (*Nipponoserica* spp., *Pseudosericania*)) is supported numerous apomorphies (Bremer support: 6, jackknife value: 98 %). Testing the hypothesis that *Pseudosericania* is a valid genus, (a) (*Nipponoserica* spp. + *Nipponoserica sulciventris*) would be paraphyletic, or (b) the clade *Nipponoserica* spp. alone (node E, exclusive *Nipponoserica sulciventris*) would be based only on a very limited number of apomorphies (Bremer support: 1, jackknife value: 26 %), namely the symmetrical parameres (30:1). The latter character, which is encountered in ancestral sericine chafers and other melolonthine lineages as well, may be plesiomorphic,

but may also appear in analogous situations where symmetric parameres have developed independently, such as in the genus *Oxyserica* Brenske, 1900. The second scenario would demand the establishment of a monotypic genus for *Nipponoserica sulciventris*, whose two unambiguous autapomorphies are also subject to homoplasy (21:2, 32:2), these being rather unsuitable for defining a genus. Further study of the Chinese fauna with the description of additional new species might help to resolve this problem more definitively.

On the other hand, the so believed “Himalayan *Nipponoserica*” (Ahrens 2000c) are obviously unrelated to *Nipponoserica*. I establish for this basal monophyletic clade a new genus *Xenoserica* gen. n.

***Xenoserica* gen. n.**

Type species. *Nipponoserica sindhensis* Ahrens, 2000 (by present designation).

Diagnosis. Body oval, dark or reddish brown, antenna yellowish, dorsal surface shiny or dull, glabrous. Antenna yellow, with ten antennomeres; club with three antennomeres. Mentum weakly elevated and flattened anteriorly, with ligular lobes fused medially but being well separated from prementum plus palpiger. Pronotum moderately wide, widest at base, lateral margins straight and subparallel in basal half, in anterior half weakly curved and convergent anteriorly, anterior angles strongly produced and moderately sharp, posterior angles right angled but strongly rounded in the tip, anterior margin weakly produced medially, with a distinct and broad marginal line, surface with microscopic setae in the punctures only; anterior and lateral borders setaceous; hypomerion distinctly carinate at base. Apical border of elytra chitinous, without short microtrichomes. Legs slender and with shiny surface; metacoxa throughout with fine adpressed setae, which are laterally much longer; metafemur shiny, sharply margined anteriorly and without a submarginal serrated line, posterior margin weakly convex, with a few strong setae medially, only weakly widened dorsally in apical half and not serrated, ventrally not serrated. Metatibia slender and long, widest at apex, dorsally longitudinally convex, with two groups of spines, basal one at one third, apical one at three fourths of metatibial length; lateral face longitudinally convex; ventrally not margined nor serrated, apex interiorly near tarsal articulation shallowly concave, nearly truncate. Tarsomeres dorsally glabrous and impunctate, ventrally with sparse, short setae; metatarsomeres ventrally with a strongly serrated ridge, beside which is a fine longitudinal carina. Parameres symmetrical, basally symmetrically produced.

Distribution. Himalaya (Fig. 83). *Xenoserica* is restricted to the West Himalaya and western Central Himalaya.

Remarks. The new genus includes *X. sindhensis* (Ahrens, 2000) comb. n., *X. pindarensis* (Ahrens, 2000) comb. n., and *X. brachyptera* sp. n.

Etymology. From latinised Greek, *xenos* - strange, unfamiliar, combined with the genus name *Serica* (*serikos* - silky).

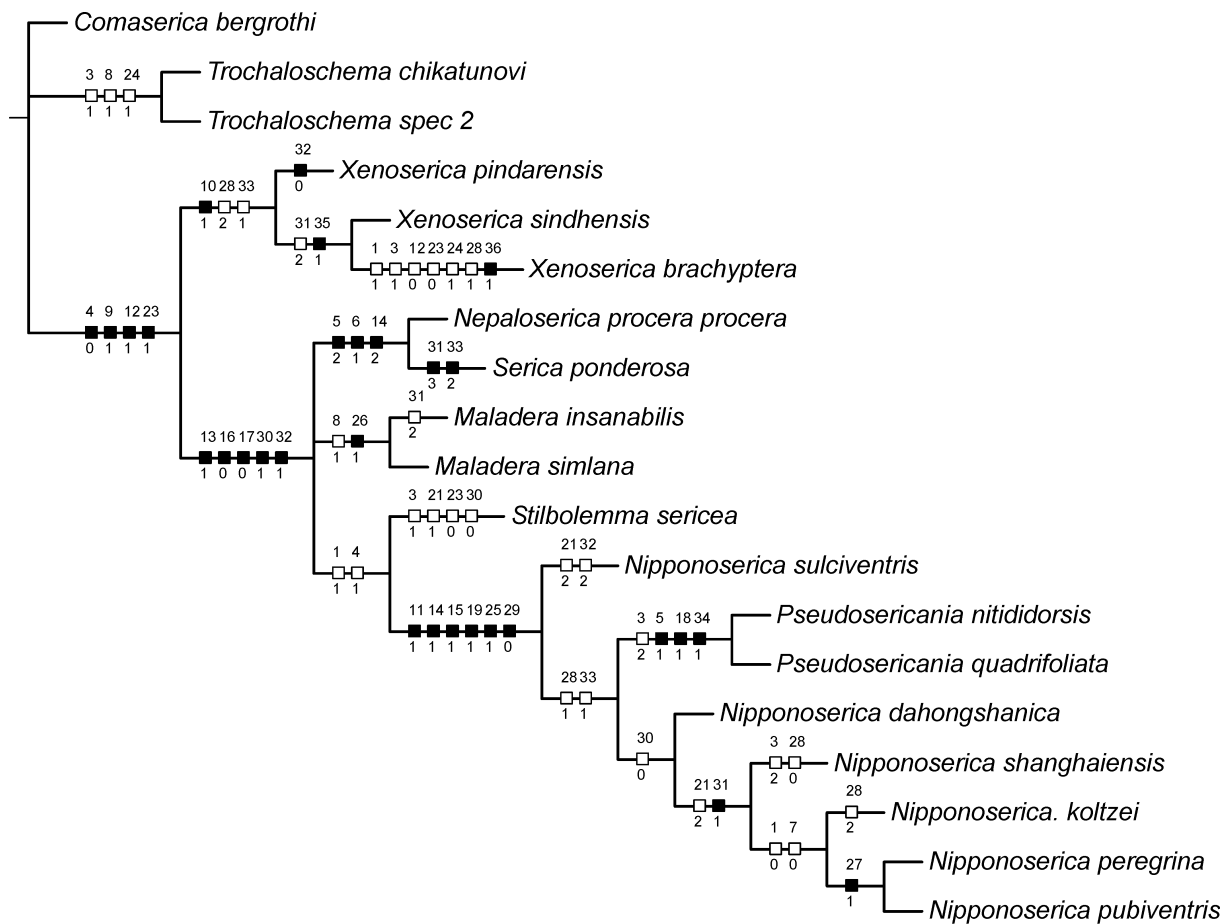


Fig. 88. Strict consensus of the two equally parsimonious trees with a length of 72 steps (CI: 0.62 and RI: 0.82) showing character changes and apomorphies mapped by state (discontinuous character states are mapped as homoplasious and only unambiguous changes are shown, unsupported nodes collapsed and using proportional branch lengths) (Full squares: non-homoplasious character states; empty squares: homoplasious character states).

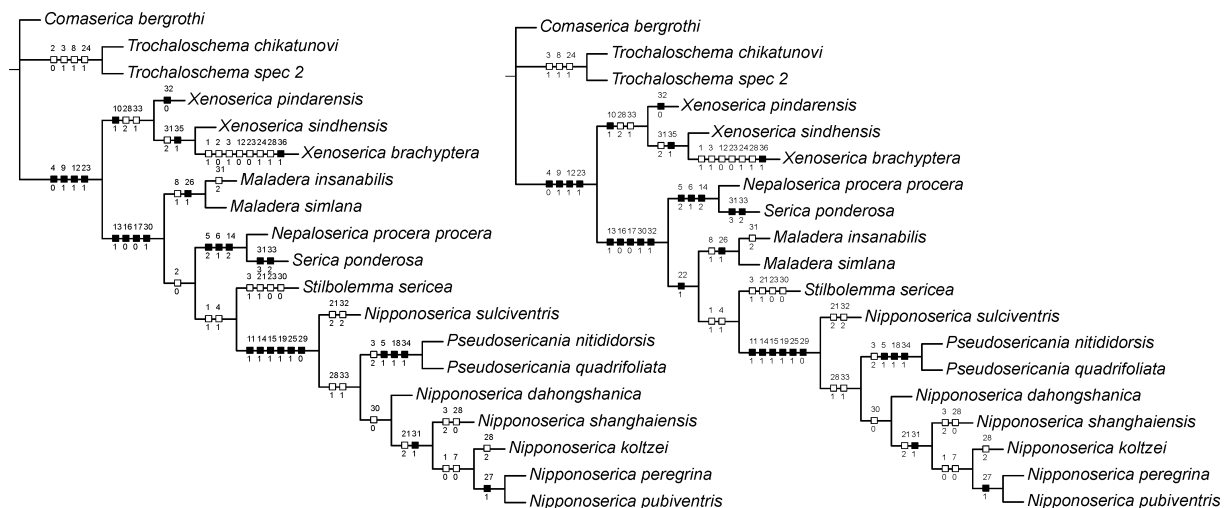


Fig. 89. The two equally parsimonious trees with a length of 72 steps (CI: 0.62 and RI: 0.82) showing character changes and apomorphies mapped by state (discontinuous character states are mapped as homoplasious and only unambiguous changes are shown, unsupported nodes collapsed and using proportional branch lengths) (Full squares: non-homoplasious character states; empty squares: homoplasious character states).

Implications for evolutive adaptations and biogeography

It seems highly probable that the genus *Nipponoserica* evolved on the Asian mainland, having its principal basal lineage there. Later, Taiwan (“*Pseudosericania*”) and the temperate northern regions (Manchuria, Japan) were invaded (clade *N. koltzei* (*N. pubiventris*, *N. peregrina*)) where speciation continued to occur. In order to answer another interesting question, due to monophyly of *Stilbolemma* + *Nipponoserica* apparent from present analysis, if *Stilbolemma* invaded North America via the Bering strait, further phylogenetic studies are needed, especially of the American lineages, and a comprehensive study considering all principal Holarctic lineages is also necessary.

Very interestingly from the viewpoint of Himalayan historical biogeography, all three representatives of *Xenoserica* are associated with main river valleys of the Himalaya, namely the Indus, Sutlej and Thakkhola (/Kali Gandaki). These valleys are very old (Garzione et al. 2000), and the rivers traversing them have continued to erode and to cross the Great Himalayan chain irrespective of very high exhumation rates (Le Fort 1996). Due to their exposure to varied climatic influences such as monsoon rains and cold northern winds, these valleys exhibit over short distances a great diversity of climatic conditions (Dobremez 1976). During extreme climatic fluctuations, isolated areas in these valleys offered refugia separated by short distances and recency of development. These arguments may lead us to assume that the occurrence of the *Xenoserica* species is a relic of a more extensive distribution. This would be also consistent with tree topology, namely their basal position within ‘modern’ Sericini. As an alternative hypothesis, one could argue for the occurrence of a more recent invasion of the Himalaya via the northern high plateaus along the large river valleys.

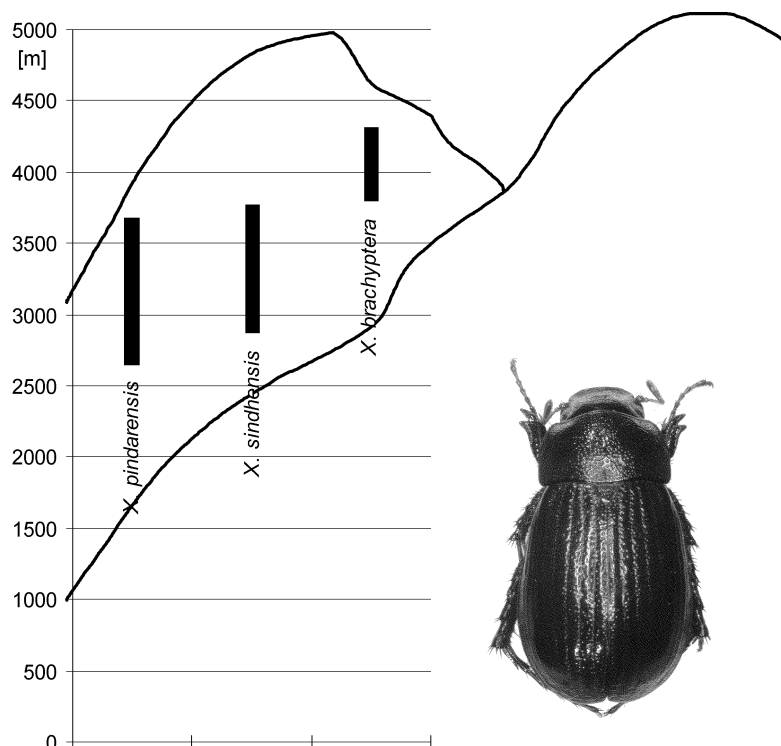


Fig. 90. The altitudinal distribution of the *Xenoserica* (= *X.*) species showing the exclusive occurrence of the new brachypterous species, *X. brachyptera*, in high altitude, which apparently has led to special morphological adaptations: diminishing of eyes size, reduction of length of antennal club, wing reduction, and loss of flight.

In contrast to the species of *Trochaloschema* of the Pamir, in which all species are brachypterous, in the Himalayan species, *X. brachyptera*, the reduction of flight apparatus is

less progressed: the elytra/ mesonotum/ scutellum are not yet affected by any reductions, and also the metanotal sclerotizations are still present (Fig. 84B, arrows), while the postnotum is completely reduced (Fig. 84B, left arrow). In *Trochaloschema* the metanotal sclerotizations are reduced (Fig. 84D, arrows) and the mesonotum is shortened, which should decrease the capacity to spread the elytra. In both flight reduction processes, the cranial portion of ventral flange of the metafurca (Fig. 84C) is reduced in size. Presumably not linked to flight reduction but to a reduction of burrowing activities is the reduced size of the interior process (p2) of the mesofurcal arm in *X. brachyptera* (Fig. 84G). This might be interpreted as a transition to something like a paraepigean life-style, taking into consideration that this species is the only one known to dwell exclusively in the alpine region (Fig. 90), where permafrost is predominant and large areas of boulders and smaller rocks exist with a complex system of subterranean interstices filled with soil.