

Phylogeny and biogeography of the lucanid beetles of the tribe Aesalini (Insecta, Coleoptera, Lucanidae), with special reference to the effect of Himalayan uplift as the vicariance event

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The lucanid tribe Aesalini (Insecta, Coleoptera, Lucanidae) consists of the three genera, *Aesalus* Fabricius, 1801, *Lucanobium* Howden et Lawrence, 1974 and *Echinoaesalus* Zelenka, 1993 (Krajcik, 2001). Of these, the genus *Aesalus* includes more than 10 species from both the Old and New Worlds, while *Lucanobium* is containing two species from South America (Araya and Yoshitomi, 2003). The genus *Echinoaesalus* has most recently been erected based on the Indonesian species, *E. jaechi* Zelenka, 1993, and afterwards, all the Southeast Asian species which had belonged to the genus *Aesalus* were moved to the genus *Echinoaesalus* (Araya et al. 1998, Zelenka 1994). In the present study, phylogenetic relationships among 22 species of the tribe Aesalini (including the genera *Aesalus*, *Echinoaesalus* and *Lucanobium*) are analyzed based on the adult morphologies (a total of 36 characters).

The resultant phylogeny demonstrates that the Aesalini is composed of two major lineages, northern Aesalini and southern Aesalini lineages. The northern Aesalini lineage is composed of three major lines: a Palearctic *Aesalus* line (containing *A. scarabaeoides* from Europe, *A. ulanowskii* from Caucasus and *A. asiaticus* from Japan), African *Aesalus* line (*Aesalus* sp. from Zaire) and a Chinese *Aesalus* line (containing *A. imanishii* from Taiwan and *A. sichuanensis* from West China). The southern Aesalini lineage contains two major lines: a Himalayan *Aesalus* and a tropical Aesalini line. The former line consists of *A. himalayicus* complex and the latter consists of two major groups: a bristly tropical Aesalini group (containing *A. satoi* from Laos, Neotropical *Aesalus* members and southeast Asian *E. matsuii* complex) and a clumpy Aesalini group (containing Neotropical *Lucanobium* and southeast Asian *E. timidus-hidakai* subgroup).

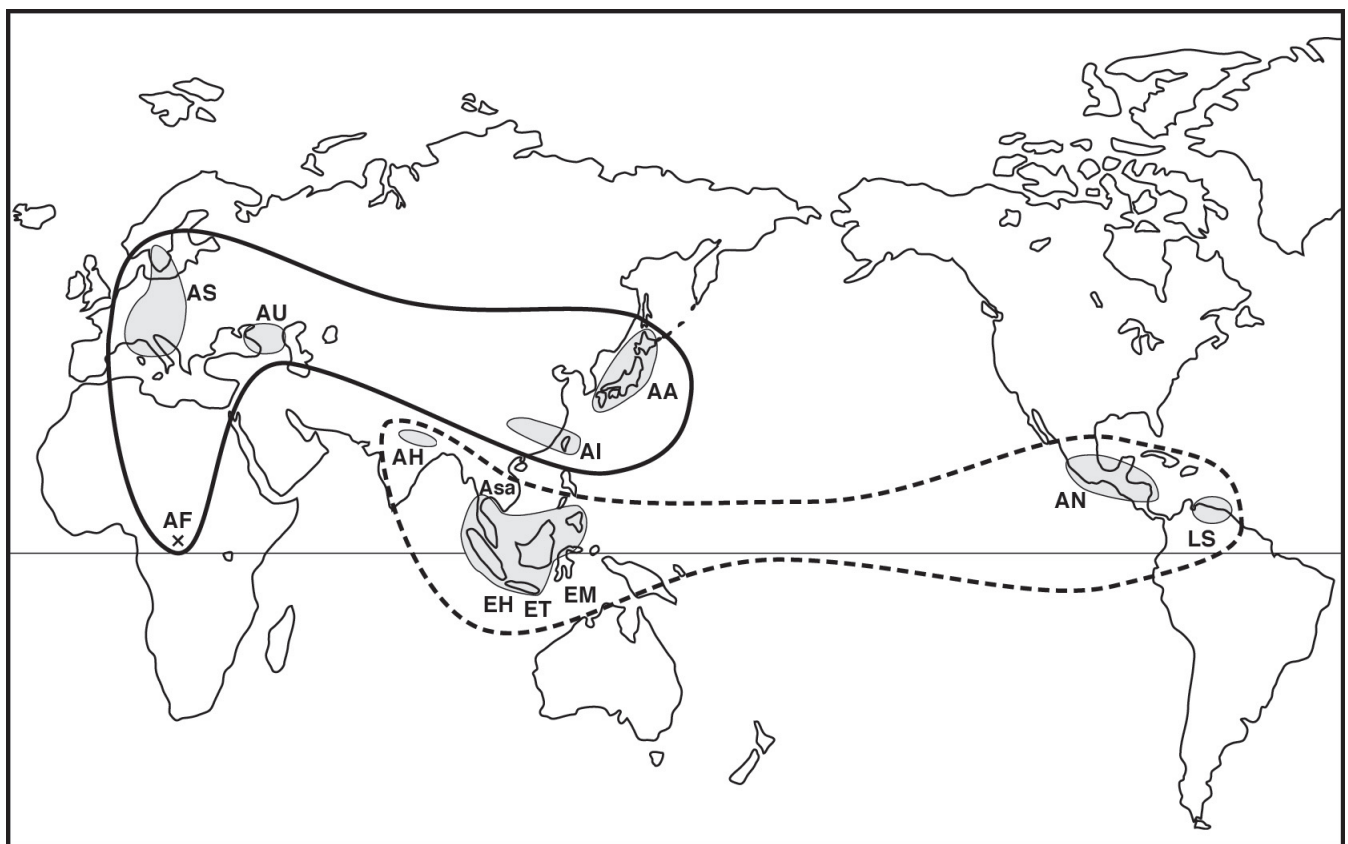


FIGURE 1. Map showing the distribution of the tribe Aesalini. AS=*A. scarabaeoides*, AU=*A. ulanowskii*, AA=*A. asiaticus*, AH=*A. himalayicus* complex, AI=*A. imanishii* complex, Asa=*A. satoi*, AN=*A. neotropicalis* complex, LS=*L. squamosum* complex, EM=*E. matsuii* complex, ET=*E. timidus* complex and EH=*E. hidakai* complex

The inferred phylogenetic patterns among the members of Aesalini indicated that the *A. himalayicus* complex and the *A. imanishii* complex, both of which showed relic distributions in the Asian Continent, retained the most ancestral character states in the northern Aesalini and the southern Aesalini lineages, respectively. Further, recently a fossil genus, *Cretaesalus* Nikolajev, 1993, belonging to the subfamily Aesalinae was described from the upper Cretaceous stratum of Kazakhstan. Based on these paleontological and neontological information, it is suggested that the ancestor of Aesalini originated in the Eurasian Continent, possibly around the Himalayas, and that Himalayan uplift, the great vicariance event against dispersal and gene flow, may strongly effect on the initial divergence between two major lineages, northern Aesalini and southern Aesalini lineages. In the southern Aesalini lineage, the Himalayan *Aesalus* line and the tropical Aesalini line were separated in the Oriental Region. In the tropical Aesalini line, the bristly and clumpy Aesalini groups were separated in Southeast Asia. Thereafter, both

the ancestor of *Lucanobium* in the clumpy Aesalini groups and the ancestor of *A. neotropicalis* complex migrated from the Old World to the New World through the Bering Land Bridge like tapirs (Mammalia, Perissodactyla).

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