

only from Java, whereas the other members, *L. birmanus* Emery, *L. kali* Rigato and *L. quadrispinosus*, are found from the Oriental region excluding the Indo-Malayan subregion. The *Pheidologeton yanoi* Forel group, similarly, is present in Indochina and Java, but absent in Borneo and Sumatra (Yamane, 2001, pers. com.). This also contributes to the lower faunal similarity between lowland rainforest in W. Java and that in Borneo / southern Malay Peninsula.

7) Restricted to Borneo

7.1) Species inhabiting lower montane oak forest (represented by *P. acantha* sp. nov., *P. kikutai* sp. nov., *P. montana*, *P. sayapensis* sp. nov., *P. submonticola* sp. nov. and *P. tenebricosa* sp. nov.)

These species have so far been found from Borneo and inhabit lower montane oak forests. They may have been derived, through habitat shift, from populations which originally inhabited lowland rainforests; or they have originated from isolated populations of premontane / lower montane species which were once widespread during glacial periods, and they have still remained confined to Borneo probably due to their lower dispersal abilities and / or scant dispersal opportunities. These species, together with the species of Pattern 5, constitute a unique *Pheidole* fauna of lower montane oak forest in N. Borneo.

7.2) Lowland tropical rainforest species (represented by *P. merimbun* sp. nov., *P. parvicorpus* sp. nov., *P. poringensis* sp. nov.).

These species, together with *P. sabahna* (Fig. 58), *P. spinicornis* sp. nov. and *P. angulicollis* sp. nov. inhabiting both lowland rainforests and lower montane oak forests, may have originated through isolations caused by glacial environmental changes (mentioned below), and they have still remained confined to Borneo probably due to their lower dispersal abilities and / or scant dispersal opportunities (initial cases of Pattern 4).

Speciation in the Indo-Malayan subregion

Based on his analysis of the present and fossil distributions of ants, Brown (1973) suggested that warm-country dominant ant taxa, such as *Pheidole* and *Crematogaster*, probably originated in tropical Africa-southern Asia and have spread explosively over the rest of the earth from about the Miocene, and that *Tetramorium*, which arose almost simultaneously, and *Camponotus*, which arose earlier in the Tertiary, may also fit this pattern in a general way.

Relatively high diversity in the Indo-Malayan subregion of *Pheidole* and of several other groups, e.g., *Camponotus* which are adapted to humid tropical habitats (Yamane, 2001, pers. com.), may have been caused partly by repeated immigrations from the continents (Pattern 6, and probably part of Pattern 5). Speciation within the subregion may also have contributed to it to a large extent. The Pleistocene refuge theory proposed by Brandon-Jones (1998) presents one possible explanation for *Pheidole* speciation in the Indo-Malayan subregion. According to this theory the multiplication of species adapted to lowland rainforests in the subregion would have been caused by repeated shrinkage and fragmentation of Indo-Malayan lowland rainforests during glacial periods and the resultant occurrence of a number of isolated populations of which some became new species. This may also be principally true for the multiplication of species adapted to premontane / lower montane forest, but here isolation events were associated with interglacial periods (mentioned above). On the other hand, species newly emerged through peripatric / allopatric speciation would have tended to spread widely