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Rove Beetles (Coleoptera: Staphylinidae) of Lanjak Entimau, Sarawak, East Malaysia

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Abstract: A study to determine the abundance of rove beetle (Coleoptera: Staphylinidae) was conducted from 15 to 28 June, 2008 at the dipterocarp forest of Lanjak Entimau, Sarawak, Malaysia. Collections were made at five sites namely Kawi River, Menyaring II, Satap, Begua and Joh River. A total of 175 rove beetles comprising of 17 species were sampled from all 5 sites of Lanjak Entimau. There was a high abundance (Margalef index, 3.097) and moderate diversity (Simpson diversity index, 0.798) of rove beetles at Lanjak Entimau. Four species were identified to species level, *Orphnebius bakerianus* Motschulscky, 1858, *Eleusis kraatzi* LeConte, 1863, *Belonuchus quadratu* Nordman, 1837, *Bledius gracilicornis* Casey, 1889. Seven species were identified to genus level *Orphnebius* sp., *Coproporus* sp., *Paederus* sp1, *Paederus* sp2, *Hesperus* sp., *Lispinus* sp., *Bledius* sp. and six species could not be identified even to genus level. Six unidentified species probably new for Science. Moderate diversity and high abundance of rove beetles at Lanjak Entimau are due to diverse habitats. Some differences in species sampled from peninsular Malaysia is explained in terms of isolation between Sarawak in Borneo island with peninsular Malaysia.

Key words: Sarawak, rove beetle, Orphnebius bakerianus, motschulscky, 1858, Hesperus sp., Lispinus sp., Bledius Gracilicornis Casey., 1889, Eleusis kraatzi LeConte., 1863, Belonuchus quadratu Nordman., 1837, Orphnebius sp., Coproporus sp., Paederus sp., Hesperus sp., Bledius sp.

INTRODUCTION

The family Staphylinidae commouly known as rove beetles includes 47,744 described species in 3,847 genera and 31 subfamilies in the world (Herman, 2001). Due to its slender elongated body with a short elytra and exposed abdomen it is not recognized as beetle by some people. Most rove beetles are predators of insects and other invertebrates, living in forest leaf litter and similar kinds of decaying plant matter. Several groups of staphylinids live as parasites of colonies of social insects such as termites, ants and leafhopper (Manley, 1997).

However, 442 species in 102 genera and 7 subfamilies are known to be confined to seashore habitats (Ahn and Ashe, 1996, 2004; Hammond, 2000; Moore and Legner, 1976). There are some taxonomic studies on fauna of Staphylinidae of Malaysia. Nomura (2005) classified and identified Pselaphitae subfamily of Staphylinidae of Malaysia. Maruyama *et al.* (2003) described a new species, *Drusilla inflatae* n sp. (Maruyama *et al.*, 2003), which mimic *Crematogaster inflate* Smith, 1957 (Hymenoptera; Formicidae) from Gombak and Endau Rompin. Hlava and Maruyama (2004) described a new genus and a new species *Malayloeblius sausai* Istner, 1993. James (2004) reported four new species of Staphylinidae *Bryothimusa hauseri* Ashe, 2004, *B. testeceipennis* Cameron, *B. catalinae* Casey and *B. algorum* Sawada.

Beetles assemblage by Chung (2004) using flight interception trap showed that Staphylinidae and Scarabaeidae were the most abundant beetle families in lowland dipterocarp forests of Sabah, East Malaysia. Similar findings was reported by Fauziah et al. (2008) for the man made lake Tasek Kenyir in peninsular Malaysia. Other recent studies on beetle abundance and diversity including on staphylinids in peninsular Malaysia were by Fauziah (2005-2008). Fourteen species from 57 rove beetles were assembled from Langkawi Island (Fauziah, 2005), 10 species from 99 rove beetles were assembled from Langgun and Dendang island (Fauziah, 2006), 10 species from 77 specimens of rove beetles were assembled in the reserved forest of Endau rompin (Fauziah, 2007). Only one species of rove beetle was collected at Lalang Island. (Fauziah, 2008). Staphylinid beetles has many roles in nature existing in every type of habitat with diets including everything except living tissues of higher plants.

A study on abundance and diversity of staphylinid at Lanjak Entimau Wildlife Sanctuary (LEWS) in Sarawak was conducted to determine that the staphylinids has not been affected by a disturbed environment. A check list of rove beetle at Lanjak Entimau will be given and the best trapping method for sampling staphylinids will be studied.

MATERIALS AND METHODS

Study Venue

Sampling sites at Lanjak Entimau (Fig. 1) were conducted at Kawi River, Menyaring II, Satap, Begua and Joh River from 15 to 28 June, 2008. The base camp was located at Sungai Katibas and long boats manned by ethic people Iban was used to travel from the base camp to the sampling sites along rapids and river.

Sampling Methods

To ensure maximum assemblage, several methods of collection was employed following Fauziah (2006). A total of twenty light traps, twenty Malaise trap, 80 pitfall traps (Fig. 2) and net sweeping were carried out from 15 to 28 June 2008. All traps were set up in the morning at 08:00 for 24 h except for light trap which was set up before nightfall, at 17:00. The generator was switched on to collect beetles attracted to light for 4 h from 19:00 to 23:00.



Fig. 1: Lanjak Entimau Wildlife sanctuary situated in Sarawak, North Borneo Island

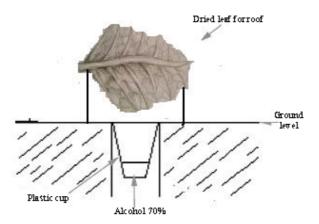


Fig. 2: Pitfall trap consisting of 9 cm diameter plastic cup containing 250 mL 70% alcohol was sheltered from rainwater with dryleaf attracts rove beetle

Table 1: A summary of Stapylinids beetles collected from five study sites in Lanjak Entiman

			Overall LEWS	Overall LEWS	Overall LEWS
Location	Species	Individual	Margalef	Simpson DI	Sharmon-weaver index
Kawirier	9	55	3.097	0.798	1.997
Joh river	10	22			
Satap	7	26			
Ведиа	12	55			
Menyaring II	7	17			
Total	17	175			

Sorting and Preservation

Staphylinid beetles were sorted to morpho species and preserved in 70% alcohol and brought back to University of Malaya for further processing. At University of Malaya, the staphylinids were pinned, dried at 40°C in oven and properly labeled.

Species Identification and Calculation of Ecological Index

Crossreference were done with collections from Department of Agriculture, Peninsular Malaysia, Kuala Lumpur and National Museum of Sarawak. Margalef index, Simpson Diversity index and Shannon-weaver index were used to calculate the abundance and diversity of staphylinid beetles as in Fauziah et al. (2008). Abundance increase proportionately to the value of Margalef index. In Simpson diversity index, diversity value is between 0 to 1 the nearer the value is to 1 the higher is the diversity. The maximum value of Shannon-weaver is 5. The bigger the value the higher is the diversity.

RESULTS

A summary of the rove beetles collected at Lanjak Entimau is given in Table 1. One hundred and seventy five specimens of rove beetles from 17 species were assembled at Lanjak Entimau Wildlife Sanctuary. Fifty five specimens from 9 species were assembled at Kawi River, 22 specimens from 10 species were assembled at Johniver, 26 specimens from 7 species were assembled at Satap River, 55 specimens from 12 species were assembled at Begua whereas 17 specimens from 7 species were sampled at Menyaring II. Combining all study sites, the abundance of rove beetles at Lanjak Entimau was high (Margalef index, 3.097) and moderately diversed (Simpson Diversity index, 0.798;

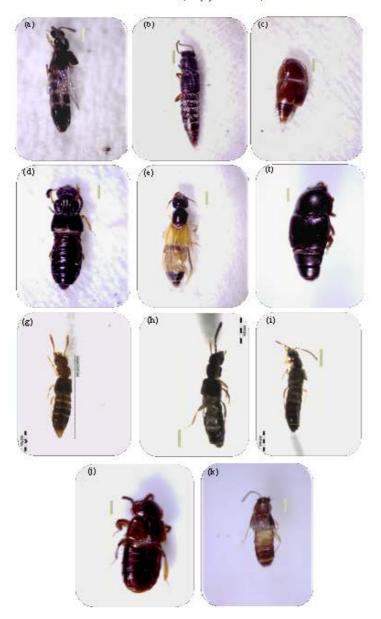


Fig. 3: The rove beetle species collected at Lanjak Entim au (a) Orphrebius sp. (length: 3.34 mm), (b) Paederus sp. (length: 2.90 mm), (c) Coproporus sp. (length: 4.05 mm), (d) Eleusis kraatzi, (length: 4.36 mm), (e) Beloruchus quadrates, (length: 4.02 mm), (f) Bledius species (length: 3.86 mm), (g) Bledius gracilicorrais, (length: 2.07 mm), (h) Lispinus sp. (length: 1.87 mm), (f) Paederus sp2, (length: 2.05 mm), (f) Orphrebius bakerianus, (length: 3.85 mm), (k) Hesperus sp. (length: 2.91 mm)

Shannon-weaver index, 1.997). Both Kawi river (n = 55) and Begua (n = 55) sampled the most number of rove beetle specimens (Table 1).

The rove beetle species collected at Lanjak Entimau are given in Fig. 3a-k. Eleven species of rove beetles were identified and are new records for Lanjak Entimau Sarawak. Four species were indentified

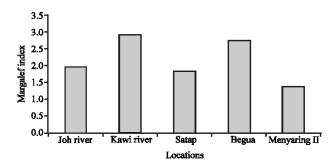


Fig. 4: Abundance of rove beetles at different location according to Margalef index

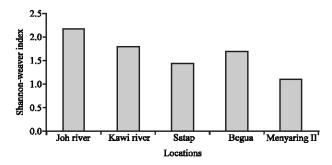


Fig. 5: Diversity of rove beetles at different location according to Shannon-Weaver index

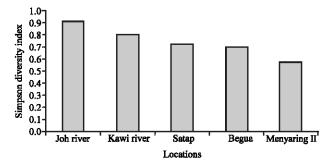


Fig. 6: Diversity of rove beetles at different location according to Simpson index

at species level, *Orphnebius bakerianus*, *Eleusis kraatzi*, *Belonuchus quadratu*, *Bledius gracilicornis*, seven species were identified at genus level *Orphnebius* sp., *Coproporus* sp., *Paederus* sp1, *Paederus* sp2, *Hesperus* sp., *Lispinus* sp., *Bledius* sp. and 6 species could not be indentified even at genus level. The six unidentified rove beetles are probably new species.

Figure 4 and 5 give the value of margalef index and Shannon weaver index indicative of the abundance and diversity of rove beetles caught at different sampling sites respectively at Lanjak Entimau. The rove beetle assemblage was most abundant at Kawi river with highest value of margalef index of 2.912 followed by Begua with margalef index of 2.745. The most diversed rove beetle caught was from Joh river (Shannon-weaver, 2.174) followed by Kawi river (Shannon-weaver, 1.785) and Begua (Shannon-weaver index, 1.68). Similar result was given using Simpson diversity index (Fig. 6). The most diverse rove beetle was found at Joh river followed by Kawi river. The nearer the value to 1 the higher the diversity value.

Table 2: Staphylinid beetle species assembled at different study sites at Lanjak Entimau.

	Location						
Species	Joh river	Kawi river	Satap	Begua	Menyaring II	Total	
Orphne bius sp.	-	-	-	1 (LT)	-	1	
Coproporus sp.	_	1 (LT)		-	-	1	
Orphne bius bakerianus	2 (PF)	1 (LT)	1 (LT)	2 (PF)	1 (PF)	7	
Motschulscky., 1858							
Paederus sp1	1 (PF)	5 (PF, LT)	-	2 (PF)	-	8	
Hesperus sp.	3 (PF, LT)	5 (PF, LT)	_	7 (PF, MT)	-	15	
Lispinus sp.	2 (MF, PF)	16 (PF, LT, MT)	10 (PF, LT)	29 (PF, LT)	3 (LT, MF)	60	
Paederus sp2	3 (PF, MT)	_	-	1 (PF)	1 (LT)	5	
Bledius sp.	2 (PF)	5 (LT, PF)	1 (LT)	1 (PF)	1 (PF)	10	
Eleusis kraatzi LeConte., 1863	_	_	1 (LT)	_	-	1	
Belonuchus quadrate	2 (PF)	-	-	-	-	2	
Nordman., 1837							
Bledius gracilicornis	1 (LT)	-	2 (PF)	6 (MT, PF)	-	9	
Casey., 1889							
Staphy 1 ^(*)	_	-		1 (LT)	-	1	
Staphy 2 ^(*)	5 (PF, LT)	17 (PF, MT, LT)	10 (PF, LT, MT)	3 (PF, LT)	11 (PF)	46	
Staphy 3 ^(*)	_	4 (PF)		1 (LT)	_	5	
Staphy 4 ^(*)	_	· -	1 (LT)	1 (LT)	_	2	
Staphy 5 ^(*)	1 (LT)	_	_		_	1	
Staphy 6 ^(*)	_	1 (PF)	-	_	_	1	
17	22	55	26	55	17	175	

LT: Light trap, MT: Malaise trap, PF: Pitfall, *Unidentified

Table 3: Staphylinid beetle species assembled at Lanjak Entimau using different trap

	Trap			
Species	Pitfall	Malaise	Light	
Orphne bius sp.	-		1	
Coproporus sp.	-	-	1	
Orphnebius bakerianus Motschulscky., 1858	5	-	2	
Paederus sp1	7	-	1	
Hesperus sp.	8	2	5	
Lispinus sp.	44	5	11	
Paederus sp2	3	1	1	
Bledius sp.	7	-	3	
Eleusis kraatzi LeConte., 1863	-	-	1	
Belonuchus quadratu Nordman., 1837	2	-	-	
Bledius gracilicornis Casey., 1889	7	1	1	
Staphy 1 ^(*)	-	-	1	
Staphy 2 ^(*)	32	4	10	
Staphy 3 ^(*)	4	-	1	
Staphy 4 ^(*)	-	-	2	
Staphy 5 ^(*)	-	-	1	
Staphy 6 ^(*)	1	-	-	
17	120	13	42	

*Unidentified

Table 2 shows that Lispimus sp. was the most abundant rove beetle at LEWS (n = 60) followed by unidentified species (Staphy 2) (n = 46) and Hesperus sp. (n = 15). Lispimus sp., was mostly sampled at Begua (n = 29). Hesperus sp., Lispimus sp., Paederus sp2, Paederus sp2, Paederus sp3, Paederus sp3, Paederus sp3, Paederus sp3, Paederus sp3, Paederus sp3, Paederus sp4, Paederus sp3, Paederus sp4, Paederus sp3, Paederus sp4, Paederus sp3, Paederus sp4, Paederus sp4, Paederus sp5, Paederus sp6, Paederus sp6, Paederus sp6, Paederus sp6, Paederus sp6, Paederus sp6, Paederus sp7, Paederus sp8, Paederus sp9, Paederus sp9,

Figure 7 shows that collection of rove beetles was most abundant (Margalef index, 3.746) and specious (Fig. 8) using Shannon-weaver index (2.225) for pitfall traps. Malaise trap collected the least abundant (Margalef index, 1.559) and the least diverse (Shannon-weaver index, 1.413). Figure 9 shows

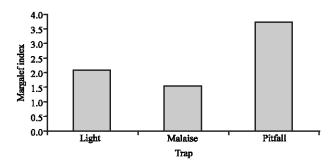


Fig. 7: Abundance of rove beetles using different trap according to Margalef index

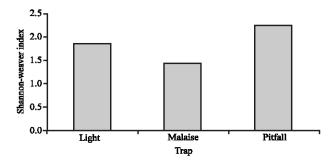


Fig. 8: Diversity of rove beetles using different trap according to Shannon-weaver index

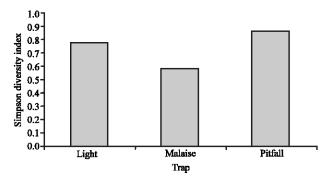


Fig. 9: Diversity of rove beetles using different trap according to Simpson diversity index

the diversity value of rove beetles collected with different traps using Simpson diversity index. Simpson diversity index also gives the highest diversity value of rove beetle by pitfall trap. Lispinus (n = 44) and Staphy 2 (n = 32) were mainly caught by pitfall traps. Pitfall was the most efficient method to collect Staphylinid beetles in this study.

DISCUSSION

Lanjak Entimau in Sarawak is situated at North Borneo Island which is separated from Peninsular Malaysia by North China Sea (Fig. 1). Among the eleven identified rove beetle species found at Lanjak Entimau, none of the species was collected at Langkawi Island (Fauziah, 2005) peninsular Malaysia nor at Lalang Island in the Straits of Malacca (Fauziah, 2008).

Eight specimens of *Paederus* sp. and three specimens of *Paederus* sp., 2 were caught at Lanjak Entimau. In peninsular Malaysia report on *Paederus* species includes those by Manley (1977) and Rahmah and Norjaiza (2008). Manley (1977) studied natural field density level, host preference, feeding pattern, behavior and biology of *Paederus fuscipes* Curtis, 1840 (Family Staphylinidae), an aggressive leaf hopper predator in rice fields in West Malaysia. (Rahmah and Norjaiza, 2008) reported on the outbreaks of *Paederus* dermatitis occurring on schoolchildren attending night tuition class due to the release of haemolymph pederin by rove beetles from genus *Paederus* when the beetle was accidentally brushed or crushed on the skin.

Orphnebius sp., Orphnebius bakerianus, Hesperus sp., Lispinus sp. and Bledius sp., which were sampled at Lanjak Entimau have not been sampled in peninsular Malaysia. This is due to isolation because Lanjak Entimau is on Borneo island. There are differences in abundance and diversity values of rove beetles between the sampling sites within Lanjak Entimau in this study.

The differences between sites at Lanjak Entimau are probably substantial enough to promote different local beetle communities with regards to both faunistic composition and diversity. Composition of staphylinids assembled by Fauziah (2007) at Endau Rompin found that Lanjak Entimau Wildlife Sanctuary has more abundant Staphylinids with Margalef index of 3.097 than Endau Rompin (Margalef index, 2.211). The Staphylinids at Selai, Endau Rompin reserved forests was more diversed (Simpson diversity index, 0.86; Shannon Weiner, 2.06) than the Staphylinids at Lanjak Entimau (Simpson diversity index, 0.79; Shannon Weiner, 1.99). This is due to many niches and different flora composition of the forests of Lanjak Entimau allows more speciation to happen. Prance (1974) and Gentry (1982) stated that the extraordinarily high species diversity of tropical forest floras and faunas is often attributed to the recent and rapid accumulation of species via high speciation rates.

Lanjak Entimau study sites are near rivers whereas samplings at Endau Rompin was conducted deep in the jungles of the reserved forest. For staphylinids, moisture and abundance of decaying organic material affects composition of its assemblage since Staphylinids like to live at margins of fresh water.

In this study, assemblage of staphylinids was most successful with pitfall trap. This is due to their small and narrow body with short elytra and flexible abdomen enabling staphylinids to live and move in ground litter (with abundant decaying organic matter) not accessible for robust and less flexible organisms. Like ground beetles, most rove beetles are predators of other insects and live on or in the soil, in ground litter, moss, or in decomposing organic matter. Thus pitfall trap was the most suitable method of sampling them.

Lanjak Entimau provides many microhabitat and niche suitable for staphylinids. Staphylinids prefer moist habitats along the margins of streams and lakes. The staphylinids also live under stone along the shores of streams, around fresh water margins, in fungi, leaf litter, plant debris, in the nests of birds, mammals, ants and termites. Thus contributes to high abundance and moderate diversity of staphylinids at Lanjak Entimau.

Fjeldsa and Lovett (1997) reported that local diversity is generated and maintained by a complex of factors such as altitude, latitude, productivity, climatic variability, age of ecosystem, predation, competition, spatial heterogeneity or the stage of the biological succession.

Tropical insects undergo seasonal changes in abundance and that the seasonal fluctuation patterns are diverse and different among species and among feeding habits (Wolda, 1978, 1980, 1988, 1989). Habitat heterogeneity is a determinant cause of biological diversity in natural ecosystems and therefore, its preservation should be a priority when planning conservation strategies (Romero-alcaraz and Avila, 2000).

Staphylinids are important biotic components of Lanjak Entimau environment occupying litter habitats that characterize forests of any age. Biodiversity research should be based on species composition and abundance useful for evaluating invertebrate communities in future conservation work in Lanjak Entimau. With high abundance and moderate diversity of Staphylinids, Lanjak Entimau should be conserved from urban development in protecting the variety of organisms including rove beetles and other insects in the forests and river margins.

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REFERENCES

- Ahn, K.J. and J.S. Ashe, 1996. Phylogeny of the intertidal aleocharine tribe Liparocephalini (Coleoptera: Staphylinidae). Syst. Entomol., 21: 99-114.
- Ahn, K.J. and J.S. Ashe, 2004. Phylogeny of the Myllaenini and related taxa (Coleoptera: Staphylinidae: Aleocharinae). Cladistics, 20: 123-138.
- Chung, A.Y.C., 2004. Vertical stratification of beetles (Coleoptera) using flight interception traps in lowland rainforest of Sabah, Malaysia. Sepilok Bull., 1: 29-41.
- Fauziah, A., 2005. The beetle assemblage of Langkawi Island. Malaysian J. Sci., 24: 185-198.
- Fauziah, A., 2006. Diversity of beetles in the North East Langkawi Islands, Malaysia. Malayan Nature J., 57: 419-431.
- Fauziah, A., 2007. Diversity and Abundance of Beetle Fauna at the South Western Side of Endau-Rompin National Park, Johore, Malaysia. In: Biodiversity at Selai, Endau Rompin, J. (Ed.). Haji Mohamed and Mohamed Zakaria, Malaysia, pp. 525-527.
- Fauziah, A., 2008. A note on the nocturnal beetle fauna of Lalang Island in straits of Malacca. Malaysian J. Sci., 27: 113-118.
- Fauziah, A., S. Ibnu and F. Fatmahjihan, 2008. The ground beetle fauna (Coleoptera: Carabidae) of Kenyir water catchment, Terengganu, Peninsular Malaysia. Pak. J. Biol. Sci., 11: 2478-2483.
- Fjeldsa, J. and J.C. Lovett, 1997. Biodiversity and environmental stability. Biodiversity Conservat., 6: 315-323.
- Gentry, A.H., 1982. Neotropical floristic diversity: Phytogeographical counections between central and South America, Pleistocene climatic fluctuations or an accident. Ann. Mossouri. Bot. Garden, 6: 557-593.
- Hammond, P.M., 2000. Coastal Staphylinidae (Rove Beetles) in the British Isles, with Special Reference to Salt Marshes. In: British Saltmarshes. Joint Symposium on British Salt Marshes Organized Between the Liunean Society of London, Sherwood, B.R., B.G. Gardiner and T. Harris (Eds.). Royal Society for the Protection of Birds and English Nature, Cardigan, London, pp. 247-302.
- Herman, L.H., 2001. Catalog of the staphylinidae (Insecta: Coleoptera). 1758 to the end of the second millenninm.V. Staphylinine group (Part 2). Bull. Am. Mus. Nat. Hist., 265: 2441-2441.

- Hlava, P. and M. Maruyama, 2004. A new genus and species of the myrmecophilous tribe Sahlbergiini from Malaysia (Coleoptera: Staphylinidae: Aleocharinae). Koleopterologische Rundschau, 74: 191-199.
- James, S.H., 2004. A new species of the intertidal staphylinid genus *Bryothimusa* and Casey from Malaysia, with an overview of geographic distribution and an annotated catalog of *Bryothimusa* (Staphylinidae: Aleocharinae: Myllaenini). Coleopterists Bull., 58: 581-597.
- Manley, G.V., 1977. *Paederus fucipes*: A predator of rice field in West Malaysia. BioControl, 22: 47-59.
- Maruyama, M., H. Yeks, R. Hashim and F. Ito, 2003. A new *Myrmecophilous* species of *Drusilla* (Coleoptera, Staphylinidae, Aleocharinae) from Peninsular Malaysia, a possible batesian mimic associated with *Crematogaster inflata* (Hymenoptera, Formicidae, Mymicinae). Jap. J. Syst. Entomol., 9: 267-275.
- Moore, I. and E.F. Legner, 1976. Intertidal Rove Beetles (Coleoptera: Staphylinidae). In: Marine Insects, Cheng, L. (Ed.). North Holland Publisher, Amsterdam, pp. 521-546.
- Nomura, S., 2005. A report on insect inventory project in tropic Asia (TAIIV) network construction for the establishment of insect inventory in tropic Asia. A Report on Insect Inventory Project in Tropic Asia (TAIIV) Network Construction for the Establishment of Insect Inventory in Tropic Asia (TAIIV) A Report of Inventory Works on the Subfamily Pselaphinae (Coleoptera, Staphylinidae) in Malaysia. JPPS., 299-336.
- Prance, G.T., 1974. Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon Basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and Lecythidaceae. Acta Amazonica, 3: 5-28.
- Rahmah, E. and M.J. Norjaiza, 2008. An outbreak of *Paederus dermatitis* in a primary school, Terengganu, Malaysia. Malaysian J. Pathol., 30: 53-56.
- Romero-Alcaraz, E. and J.M. Avila, 2000. Landscape heterogeneity in relation to variations in epigaeic beetle diversity of a Mediterranean ecosystem. Implications for conservation. Biodiversity Conservat., 9: 985-1005.
- Wolda, H., 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. J. Amm. Ecol., 47: 369-381.
- Wolda, H., 1980. Seasonality of tropical insets. I. Leaf hoppers (Homoptera) in Las Cumbres, Panama. J. Anim. Ecol., 49: 277-290.
- Wolda, H., 1988. Insect seasonality: why?. Annu. Rev. Ecol. Syst., 19: 1-18.
- Wolda, H., 1989. Seasonal cues in tropical organisms. Rainfall? Not necessarily! Oecologia, 80: 437-442.