Ant diversity as a direct and indirect driver of Pselaphinae beetle functional diversity in tropical rainforests, Sabah, Borneo

Elizabeth Psomas
March 2015

Declaration

The Soil Biodiversity Group, Life Sciences Department, Natural history Museum, London, provided the specimens of leaf litter Pselaphinae beetles for analysis. Volunteers in the Soil Biodiversity Group sorted the specimens to family and subfamily prior to this investigation. I identified all Pselaphinae beetles recorded in this study to morphospecies. Specialist taxonomist Joseph Parker identified all morphospecies to tribe and genus. I carried out all morphometric analyses on the Pselaphinae morphospecies using a compound microscope. I personally imaged and edited all the morphospecies recorded using scan electron microscopy and compound light microscopes.

I received input and suggestions by my supervisor throughout my project, including the representation and interpretation of the results, and writing of this thesis.

Elizabeth Psomas, 26th March 2015

Supervisor: Dr. Paul Eggleton (Researcher and Head, Soil Biodiversity Group, Natural History Museum, London)

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Abstract. 1. Pselaphinae beetles are tremendously diverse in tropical Asia with many exhibiting myrmecophily. The rainforests of Borneo have experienced unprecedented degradation as a result of extensive logging and conversion to oil palm. This study investigates the functional diversity of Pselaphinae beetles in response to ant abundance and ant genus richness across two old growth rainforests (Danum and Maliau) and one twice-logged rainforest (SAFE).

2. The leaf litter Pselaphinae beetles were identified to morphospecies then tribe and genus. Morphometric analysis on selected functional traits of Pselaphinae beetles along with scan electron microscopy allowed detailed morphological features to be analyzed.

3. Pselaphinae beetle community composition is strongly associated with site environmental conditions and significantly differed between old growth rainforests and twice-logged rainforest. Interestingly, Pselaphinae beetle composition also varied between the two old growth rainforests indicating high habitat-specificity. Pselaphinae myrmecophile functional traits are significantly associated with old growth rainforest site Danum, indicating there is more probable myrmecophile Pselaphinae beetles in Danum. Functional diversity increased as ant abundances and ant genus richness increased across all three sites.

4. The differences of Pselaphinae beetle community composition and more specifically probable myrmecophile beetle composition across all three sites, indicates the importance of understanding functionally important species and the their effects on ecosystem functioning, particularly in vulnerable habitats.

Keywords. Pselaphinae beetle, myrmecophily, functional diversity, community composition, Sabah, Borneo.

Introduction

The Pselaphine beetles (Family: Staphylinidae, Subfamily: Pselaphinae) are a tremendously species-rich and diverse group of leaf-litter inhabitants, particularly in Tropical Asia (Nomura & Mohamed, 2008; Chung *et al*., 2000). There are 8,890 described extant species in 1,220 genera worldwide, of which 123 species have been recorded from Borneo (Nomura & Mohamed, 2008), with many more yet to be recorded. Pselaphinae beetles are small predators (<1mm to 3mm in body length) feeding on a variety of soil invertebrates (Parker & Maruyama, 2014; Chandler, 2001).

It is known that many Pselaphinae beetles are myrmecophiles (Park, 1942). Myrmecophily is a biological association that forms between ants and a diverse number of organisms, including Fungi (Ruiz-Gonzalez *et al.,* 2011), Lepidoptera (Kaminski & Carvalho-Filho, 2011) and Coleoptera (Maruyama *et al.,* 2014). The association may be facultative, a casual association in which ants occasionally tend to the myrmecophile guest (Geiselhardt *et al.,* 2007). On the other end of the spectrum, myrmecophiles may be entirely dependent on the ant hosts during particular life-cycle stages and are termed obligates (Geiselhardt *et al.,* 2007; Mynhardt, 2013). Obligate myrmecophiles typically exhibit trophallaxis (liquid-feeding), a unique feeding behaviour articulated by the ants to the beetle (Mynhardt, 2013; Parker & Grimaldi, 2014). This is evident in the Pselaphinae tribe Clavigerini (Chandler, 2001). Other ant associations range from mutualism to parasitism with some organisms demonstrating multiple degrees of ant associations within their life cycle (Geiselhardt *et al.,* 2007). Myrmecophily is an evolutionary phenomenon that has proliferated concomitant with the diversification of ants (Parker & Grimaldi, 2014). Myrmecophiles have successfully evolved morphological characteristics that have allowed them to socially integrate and exploit ant nest resources (Akino, 2008). Currently, 35 beetle families are known to be associated with ants, including the Pselaphinae, which display a diverse set of morphological adaptations in relation to the varying degree of their associations (Mynhardt, 2013; Parker & Grimaldi, 2014).

In a study by Yin & Li (2013) new species of myrmecophilous Pselaphinae beetles in the tribe Batrisini were identified which represent the first record of Pselaphinae beetles to be associated with *Ondontomachus* ants. Myrmecophilous Pselaphinae beetles have also been recorded to be associated with *Lasius* ants, in China (Yin & Li, 2015). Many Pselaphinae tribes including Cyathigerini (Sugaya *et al.,* 2004), Batrisini (Yin & Li, 2013) and Euplectini (Parker & Maruyama, 2013) have all been recorded to form ant associations. However, given

their small size and sheltered habitats, behavioural interactions with ants have proven difficult to observe and record. Therefore, there is very little, if any, behavioural data on Pselaphinae ant-beetle associations to complement the morphological studies.

Pselaphinae beetles display habitat-specific requirements whether it is within leaf litter, woody debris or inside ant nests (Chandler, 2001; Nomura & Mohamed, 2008). Their ecological and functional importance has made them suitable candidates for many conservation studies particularly concerning the impact of rainforest disturbances on biodiversity (Sakchoowong *et al.,* 2008; Chung *et al.,* 2000; Edwards *et al.,* 2014). Southeast Asia is one of the worlds most threatened biodiversity hotspots (Hoffmann *et al.,* 2010) as a result of human-modified land-cover changes (Edwards *et al.,* 2014). The island of Borneo has experienced extensive forest degradation as a result of industrial-scale timber extraction and conversion to oil palm, since the early 1970's (Gaveau *et al.,* 2014). Gaveau *et al.* (2014) reported 39.5% of the native forests in Sabah, Borneo have been lost as a result of intensive logging. Bioindicators, including ants and beetles, have proven to be effective predictors of the response of other taxa to logging and oil palm (Edwards *et al.,* 2014). Disturbances in ecosystem properties such as logging, greatly impact the abundance and distribution of functionally important species (Hooper *et al.,* 2005). A study by Woodcock *et al.* (2011) reported fewer ant species occurrences and lower ant species richness in twice-logged rainforest, compared with natural forests. Furthermore, Tawatao *et al.* (2014) also reported lower ant species richness in poor quality forest habitats referred to as 'habitats of critical biodiversity or social value' (HCVs) compared with 'virgin jungle reserves' (VJRs).

There have been very few studies, if any, examining the functional diversity of Pselaphinae beetles between primary old growth forest and disturbed twice-logged rainforests. Sakchoowong *et al.* (2008) demonstrated significant differences in species richness and abundance of Pselaphinae beetles between primary and disturbed habitats, in Thailand. However, the study did not look at the functional diversity of Pselaphinae beetles or more specifically at myrmecophilous Pselaphinae beetles. Therefore, investigating the biology and community composition of functionally important species such as the Pselaphinae beetles will enable better understanding on ecosystem functioning, particularly across different levels of habitat disturbance.

This study will contribute to an experimental manipulation study conducted in Sabah, Borneo, where ant communities are suppressed with targeted insecticides. The study will examine the functional traits of Pselaphinae beetles in response to ant-suppression treatment

and control plots in order to assess the degree to which traits associated with myrmecophily and surface-foraging predation are affected by the treatments.

In the current study, functional diversity of the Pselaphinae beetles will be measured by a selected source of functional traits associated with myrmecophily and through accurate morphometric analysis. Pselaphinae beetle specimens sampled prior to ant-suppression treatments have been used to test the following hypotheses:

1) Environmental variables influence Pselaphinae beetle composition between old growth and logged rainforest sites.

2) Functional traits of Pselaphinae beetles associated with myrmecophily influence their community composition in relation to environmental variables.

3) Functional diversity of Pselaphinae beetles increases in the presence of high ant abundance and ant genus richness.

Methods

The Soil Biodiversity Group, Life Sciences Department, Natural history Museum, London, provided the specimens of leaf litter Pselaphinae beetles for analysis. All sampling was conducted prior to this investigation, between September and October 2012 in Sabah, Malaysian Borneo.

Study site

Three study sites were selected: two old growth rainforests located in (1) the Maliau Basin Conservation Area ($4^0$49'N, $116^0$54'E) and (2) the Danum Valley Conservation Area ($4^0$55'N, $117^0$40'E) and a logged rainforest area established as part of a large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems (SAFE Project) (Ewers *et al*., 2011). All sampling sites located within SAFE have been through two rotations of selective logging while Maliau Basin and Danum Valley Conservation Areas have never been logged (Ewers *et al*., 2011).

Sampling methods

The *Winkler bag extraction* method was used in order to sample leaf litter macrofauna (see Krell *et al*., 2005 for a discussion on this method). The Pselaphinae beetles (Coleoptera: Staphylinidae: Pselaphinae) inhabit forest leaf-litter (Nomura & Mohamed, 2008; Sakchoowong *et al*., 2008) therefore the *Winkler bag extraction* method provides the most efficient representation of Pselaphinae beetle diversity for the purpose of this study. Leaf litter samples collected were hung in Winkler bags for three days (Carpenter *et al*., 2012). A total of 15 1m^2 quadrats of leaf litter were sieved at each plot in all three sites, at 7m intervals along a 100m transect. A range of abiotic environmental variables was recorded at each plot across all three sites. Soil moisture, soil temperature and canopy cover (using a spherical densitometer) were measured by following the methodology of Carpenter *et al*. (2012), additionally spatial environmental variables longitude and latitude were also measured.

Pselaphinae beetle Identification

The leaf litter samples were taken to the laboratory and the Pselaphinae beetles were separated and stored in 100% ethanol for analyses. Specimens were identified to Family and subfamily level using the key of A Y. C. Chung (A Y. C. Chung, unpublished manual for Bornean beetle identification (Coleoptera) family identification) prior to this investigation. At the start of my research, parataxonomic sorting methods were initially used to identify specimens to *recognizable taxonomic units* (RTUs), also known as morphospecies, based on external morphological characteristics of specimens (Hammond, 1994), hereafter referred to as morphospecies. This method has been widely adopted as a surrogate for species level taxonomic identification in many ecological studies (Oliver & Beattie, 1996; Derraik *et al.*, 2002; Gardner-Gee *et al.*, 2015; Baker *et al.,* 2004). Initially, sorting proceeded by following a key of Danum Valley Pselaphinae morphospecies identified by (Daniel Hall, unpublished), in which morphospecies were labeled alphabetically. Additional new morphospecies found in Danum, SAFE and Maliau, not represented on the list were labeled numerically. The external morphological characteristics of the head, eyes, mandibles, antennae, pronotum, elytra, abdomen and legs were carefully examined, specifically examining the shape and size of each character. Morphospecies were then identified to tribe and genus by specialist taxonomist (see acknowledgements). Coleoptera specialists Peter M. Hammond and Roger Booth (Natural History Museum, London) also examined the morphospecies identified in this study. However, due to the tremendous species diversity of Pselaphinae beetles in Tropical Asia, much of which remains unknown (Nomura & Mohamed, 2008), not all morphospecies could be identified to genus level and some tribe identities remain questionable. A total of 42 morphospecies were recorded across all three sites (Table 2). Voucher specimens were mounted, labeled and deposited in the Natural History Museum, London.

Morphometric analysis

In order to assess functional diversity of Pselaphinae beetles functional traits were selected based on an extensive literature review and are presented in Table 1. Five quantitative morphological traits were measured using a compound microscope (WILD HEERBRUGG Switzerland M5-64489) at a magnification of x25, using an ocular micrometer with a scale interval of 0.1mm. All measurements were recorded in millimeters. Total body length (TBL) was measured from the anterior clypeal margin to the posterior margin of the last abdominal

tergite and body width (BW) refers to the maximum width of the abdomen. Six qualitative morphological traits were also recorded as presence or absence data. Antennomere expansion was recorded by numbering individual antennomeres (antennomere 1 most proximal to the head and antennomere 11 most distal to the head). The terminology used to describe the foveal patterns follows Chandler, (2001).

Table 1. Summary of Functional traits selected for measuring Pselaphinae beetle Functional diversity.

Abbreviation	Trait	Data type	Functional link	Evidence
TBL	Total body length	Quantitative	Myrmecophily, microhabitat	Parker & Maruyama (2013)
BW	Body width	Quantitative		
AL	Antennae length	Quantitative		Yin & Li (2013); Parker & Grimaldi (2014)
TASL	Terminal antennal segment length	Quantitative		
TASW	Terminal antennal segment width	Quantitative	Myrmecophily	Maruyama *et al.,* 2014
AN	Antennomere number	Qualitative	Myrmecophily	Geiselhardt *et al.* (2007)
AE	Antennomere expansion	Qualitative		
HC in TAS	Hollow cavity in terminal antennal segment	Qualitative		
T	Trichomes	Qualitative	Myrmecophily	Parker & Grimaldi (2014)
S	Sensilla	Qualitative	Tactile & olfactory	Schooman *et al.* (2008)
F	Foveae	Qualitative	Evolutionary trend towards loss in myrmecophiles	Park (1942); Chandler (2001); Parker & Maruyama (2013)
Bef	Basal elytral foveae	Qualitative	Evolutionary trend towards loss in myrmecophiles	Park (1942); Chandler (2001); Parker & Maruyama (2013)

Beetle imaging

Initial dorsal view images of all morphospecies were taken using an Axioskop compound light microscope and EOS 700D Canon camera (at x10 and x4 magnifications) at the Sackler Biodiversity Imaging lab, Natural History Museum, London. Each image taken was constructed by applying a digital imaging processing technique, referred to as focus stacking, using Helicon Focus 5.3 software. This technique allows for multiple images to be taken at different focus distances in order to reconstruct a single image with a greater depth of field (Riedel, 2005).

For SEM (Scan Electron Microscopy) analysis, specimens were examined with a LEO 1455VP SEM microscope at the Imaging and Analysis Centre, Natural History Museum, London. The mounted voucher specimens of each morphospecies was placed onto a stage then inserted into the microscope chamber. The specimens were not coated for SEM analysis therefore a low vacuum chamber setting was selected for non-conductive specimens. The micrographs obtained by this instrument were used to identify the presence or absence of the following key morphological features: hollow cavity in the terminal antennal segment, trichomes, sensilla and foveae. Foveal patterns mapped were only recorded from the dorsal or side view, due to the manner in which the specimens were mounted. Micrographs were edited using Adobe Photoshop CS2 version 9.0 software.

Statistical analysis

An ordination analysis, constrained Redundancy Analysis (RDA) was used to assess the association of various site environmental variables with Pselaphinae beetle composition and functional traits. Axes were constrained by environmental variables selected out by initial Monte Carlo permutation tests. All data for morphospecies abundance were $\log_{10} +1$ transformed before analysis to reduce the influence of morphospecies with high abundances (ter Braak & Smilauer, 2014), ant abundance and ant genus richness were also $\log_{10} +1$ transformed before analysis and used as explanatory (environmental) data. The presence of the functional trait 'sensilla' was found on all Pselaphinae beetles sampled and was therefore not included in the functional trait analysis. The following environmental variables were tested: Temperature, soil moisture, canopy cover, longitude, latitude, ant abundance, ant genus richness and site (SAFE, Danum and Maliau), however only significant variables

(P<0.05) were included in the ordination plots. The statistical significance at each step was tested using a Monte Carlo permutation test (999 random permutations), testing the null hypothesis that, morphospecies composition and functional traits are independent of the environmental variables. Unconstrained Principal Component analysis (PCA) of morphospecies abundance was initially carried out prior to RDA, in order to test how much of the overall variation in morphospecies abundance is explained by the environmental data. All ordination analyses were conducted in CANOCO version 5.0 (2012).

Beta diversity was also calculated in order to measure the variation in morphospecies composition across all three sites. Two measures of beta diversity were calculated, the netestedness index (β_{SNE}) (nestedness) and the Simpsons index of dissimilarity (β_{SIM}) (turnover of morphospecies) (Baselga & Orme, 2012). Beta diversity was calculated using the *betapart* package in R (Baselga *et al.,* 2013).

Functional diversity (FD) was measured using Rao's quadratic diversity index (Rao, 1982) in CANOCO version 5.0 (2012). The Rao coefficient combines measurements of species relative abundance and the pairwise differences between two individuals of a given species, identified as qualitative or quantitative measurements (Ricotta, 2005; Ricotta & Moretti, 2011; Rao, 2010). The pairwise differences in this study are expressed as functional traits (both quantitative and qualitative measurements were included in the analysis). Functional diversity values obtained in CANOCO were used to plot General Linear Models (GLMs) in RStudio (version 0.98.1087 – © 2009-2014 RStudio, Inc.). GLMs were used to assess the response of Pselaphinae beetle functional diversity (Rao) to ant genus richness and abundance across the three sites sampled. Ant abundance and ant genus richness data was log transformed in R before GLM analysis. Ant genus richness and abundance data was taken from leaf litter samples collected from the same plots and sites during the same sampling period as the beetles, and were acquired by (Thomas Bell, unpublished).

Results

A total of 613 Pselaphinae beetles were sampled, across all three sites, representing 12 tribes and 42 morphospecies (Table 2). The abundance of each Pselaphinae tribe recorded differed considerably, even at a morphospecies level (Table 3). Probable myrmecophile morphospecies comprising 194 individuals (31.6%) were recorded from 6 different tribes. Morphospecies in the tribe Cyathigerini were numerically dominant myrmecophiles in the logged rainforest site (SAFE), comprising 80 individuals (41.2%) of the total probable myrmecophiles recorded. The least abundant morphospecies (7, 8, 13, 17, PH, AA, AB, AC and R) account for 1.5% of the total Pselaphinae beetles recorded and are represent by just one individual.

Table 2. List of all 42 morphospecies recorded from SAFE, Danum and Maliau.

Morphospecies	Tribe	Genus	Myrmecophile
A	Batrisini	Indet	Unknown
C	Trichonychini	Bibloporus?	Non-myrmecophile
D	Cyathigerini	Plagiophorus	Facultative
E	Arnyllini	Harmophorus	Facultative
F	Tmesiphorini	Pseudophanias	Possible
G	Cyathigerini	Plagiophorus	Facultative
H	Proterini	Mechanicus?	Non-myrmecophile
I	Cyathigerini	Plagiophorus	Facultative
J	Batrisini	Indet	Unknown
L	Batrisini	Batrisocenus/Batrisoplisus group	Unknown
N	Batrisini	Mnia?	Unknown
O	Trichonychini	Aphilia	Non-myrmecophile
P	Hybocephalini	Apharinodes	Non-myrmecophile
R	Proterini	Mechanicus	Non-myrmecophile
Q	Batrisini	Batrisocenus/Batrisoplisus group	Unknown
S	Batrisini	Cratna	Unknown
T	Tyrini	Horniella/Hamotopsis?	Possible
U	Batrisini	Mnia?	Unknown
V	Batrisini	Cratna?	Unknown
W	Cyathigerini	Plagiophorus	Facultative
Y	Tyrini	Pselaphodes?	Non-myrmecophile
Z	Cyathigerini	Plagiophorus	Possible
PH	Clavigerini	Pseudacerus	Obligate
AA	Batrisini	Sathytes	Unknown
AB	Tyrini	Pselaphodes?	Non-myrmecophile
AC	Pselaphini	Curculionellus	Non-myrmecophile
1	Clavigerini	Cerylambus	Obligate
2	Bythinoplectini	Indet	Non-myrmecophile
3	Bythinoplectini	Indet	Non-myrmecophile
4	Bythinoplectini	Indet	Non-myrmecophile
5	Brachyglutini	Baraxis	Unknown
6	Batrisini	Cratna	Unknown
7	Batrisini	Indet	Unknown
8	Proterini?	Mechanicus?	Non-myrmecophile
9	Batrisini	Indet	Unknown
11	Tmesiphorini? Tyrini?	Enantius?	Possible
12	Hybocelaphini	Apharinodes	Non-myrmecophile
13	Trichonychini	Aphilia?	Non-myrmecophile
15	Brachyglutini	Batraxis	Unknown
17	Proterini	Mechanicus	Non-myrmecophile
18	Trichonychini/ Euplectin?	?	Non-myrmecophile
19	Batrisini	Diagus?	Possible

Table 3. Pselaphinae beetle abundances recorded in each tribe and morphospecies (>30 individuals) across all three sites including the percentage that each tribe and morphospecies represents out of the total Pselaphinae beetles recorded.

Taxonomic level	Number of individuals	Percentage (%)
Tribe		
Batrisini	287	46.8
Trichonychini	89	14.5
Cyathigerini	80	13.1
Tmesiphorini	55	8.9
Arnyllini	35	5.7
Tyrini	18	2.9
Bythinoplectini	18	2.9
Proterini	9	1.5
Brachyglutini	8	1.3
Hybocelaphini	7	1.1
Clavigerini	6	0.9
Pselaphini	1	0.16
Morphospecies		
Q	147	23.9
C	69	11.2
N	51	8.3
F	50	8.2
I	35	5.7
E	35	5.7
Z	33	5.4

Pselaphinae beetle composition

Maliau leaf litter samples recorded the highest abundance of Pselaphinae beetles, comprising 241 individuals, followed by SAFE with 215 individuals and Danum with 160 individuals. Although Danum recorded the fewest Pselaphinae beetles, probable myrmecophile morphospecies represented by 71 individuals account for 44.4% of the total Pselaphinae beetle abundance in Danum. In comparison, 73 individuals (33.9%) represent probable myrmecophile morphospecies abundance in SAFE and 49 individuals (20.3%) represent probable myrmecophile morphospecies in Maliau. There is a high turnover (β_{sim}) of Pselaphinae morphospecies but low nestedness (β_{sne}) across all three sites (Fig. 1).

Pselaphinae beetle composition was significantly associated with site environmental variables (Fig. 3). The RDA biplot shows logged rainforest site SAFE ($F=1.6$, $P=0.091$) to be separated from old growth rainforest sites Danum ($F=1.8$, $P=0.053$) and Maliau ($F=2.5$, $P=0.014$) (axis 2). Interestingly, Danum and Maliau are also significantly separated (axis 1). Pselaphinae beetle composition is therefore strongly influenced by old growth rainforest

habitats (Danum and Maliau) compared with logged habitat (SAFE) (Fig. 2b). Eigenvalues for axis1 and axis 2 obtained by RDA analysis are lower than eigenvalues obtained in PCA analysis (Table 4). This indicates that the environmental variables selected do no explain all the variation observed in morphospecies composition across all three sites.
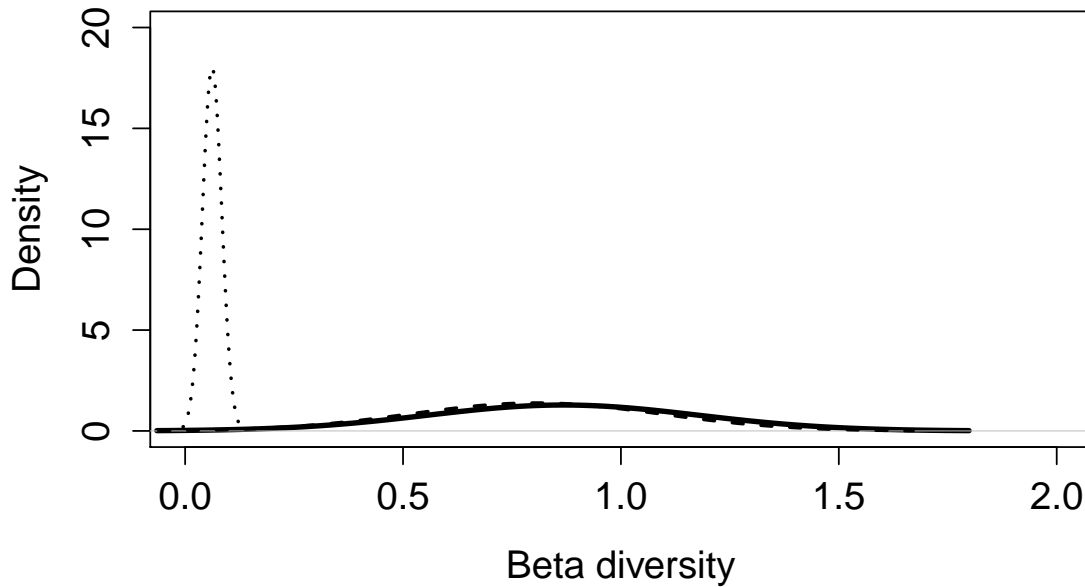
Fig. 1. Beta diversity measured by Simpsons index of dissimilarity of Pselaphinae morphospecies across all three sites (SAFE, Danum and Maliau). Overall Sorenson diversity (solid line) is a combination of Simpson's diversity index (dashed line) and nestedness diversity (dotted line).
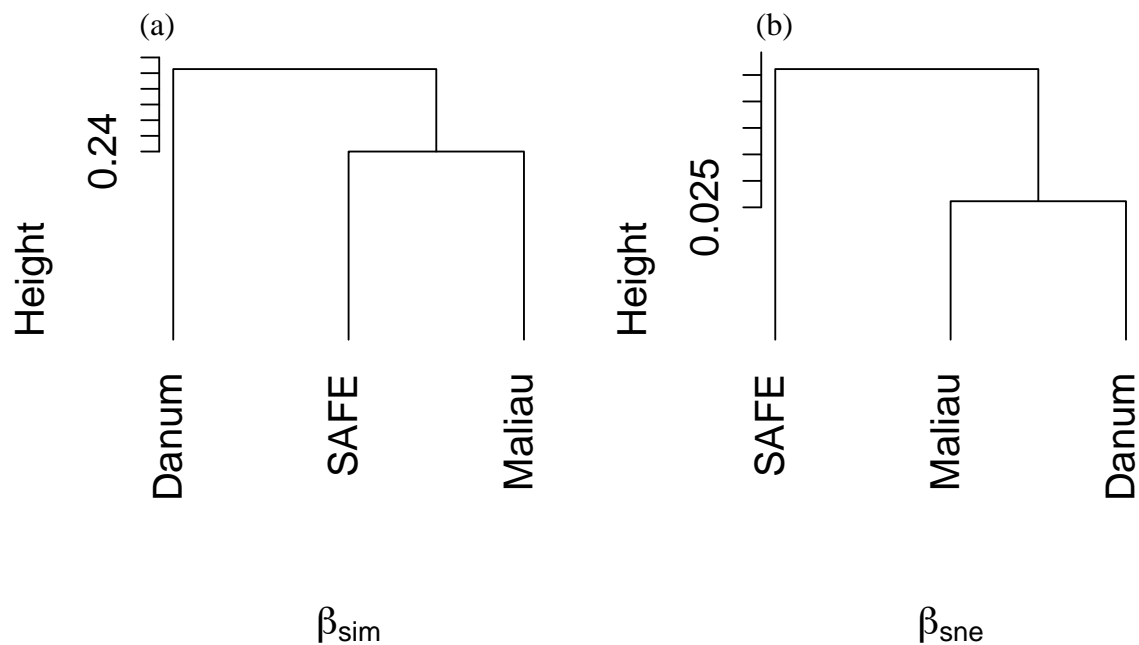
Fig. 2. Clustering dendrogram-representing dissimilarities of (a) morphospecies turnover (β_{sim}) and (b) morphospecies nestedness (β_{sne}), across all three sites.

Table 4. Statistical values obtained by PCA for morphospecies composition across all three sites and RDA for morphospecies abundance and environmental variables across all three sites.

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Unconstrained PCA				
Eigenvalues	0.2751	0.1430	0.1078	0.0799
Explained variation (cumulative)	27.51	41.82	52.60	60.59
Constrained RDA				
Eigenvalues	0.1218	0.1019	0.0611	0.1900
Explained variation (cumulative)	12.18	22.37	24.48	47.48
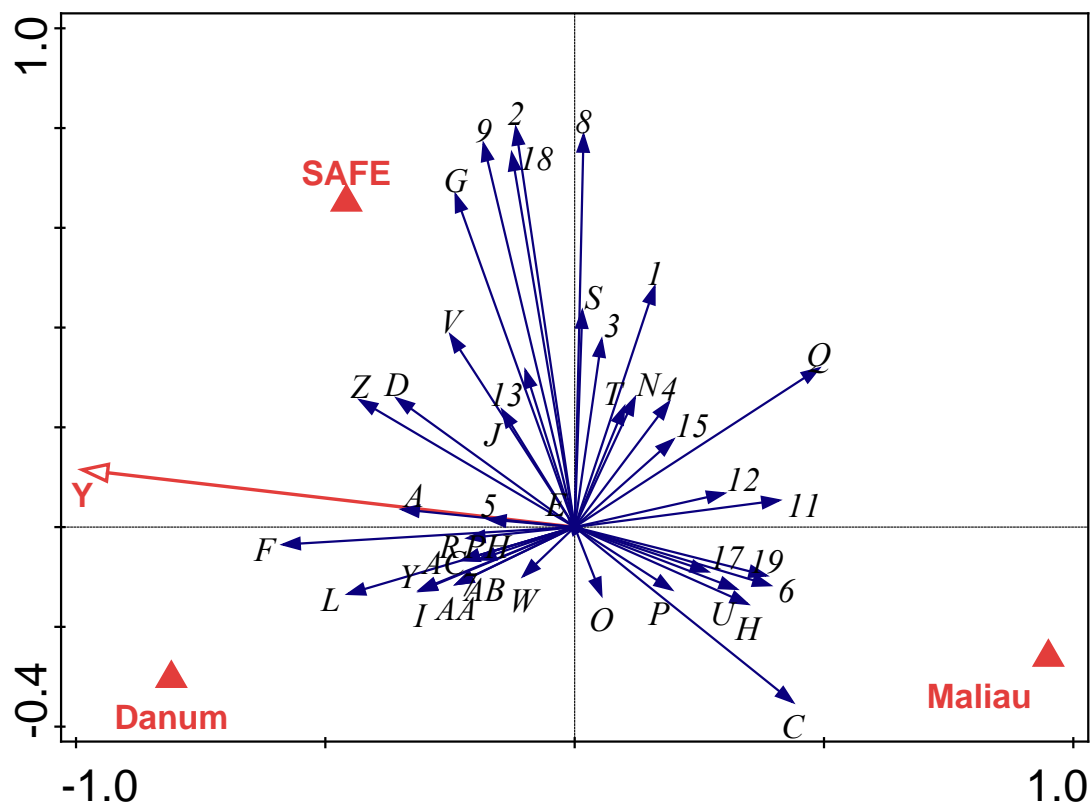
Fig. 3. Redundancy Analysis (RDA) ordination diagram of morphospecies and environmental variables. See table 2 for morphospecies tribe and genus names.

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Pselaphinae myrmecophile functional traits were significantly associated with old growth rainforest, Danum and environmental conditions (Fig. 4). Myrmecophilous Pselaphinae beetles (M) show a strong positive correlation with increasing body length (TBL), reduced number of foveae (Bef 1 and Bef 2), terminal antennal segment width (TASW) and the presence of trichomes (TP), all of which are strongly influenced by spatial environmental variables (longitude and latitude). Non-myrmecophilous (NM) Pselaphinae beetles are negatively associated with spatial environmental variables (longitude and latitude) and Danum, indicating there are more myrmecophilous Pselaphinae beetles in Danum than Maliau or SAFE.
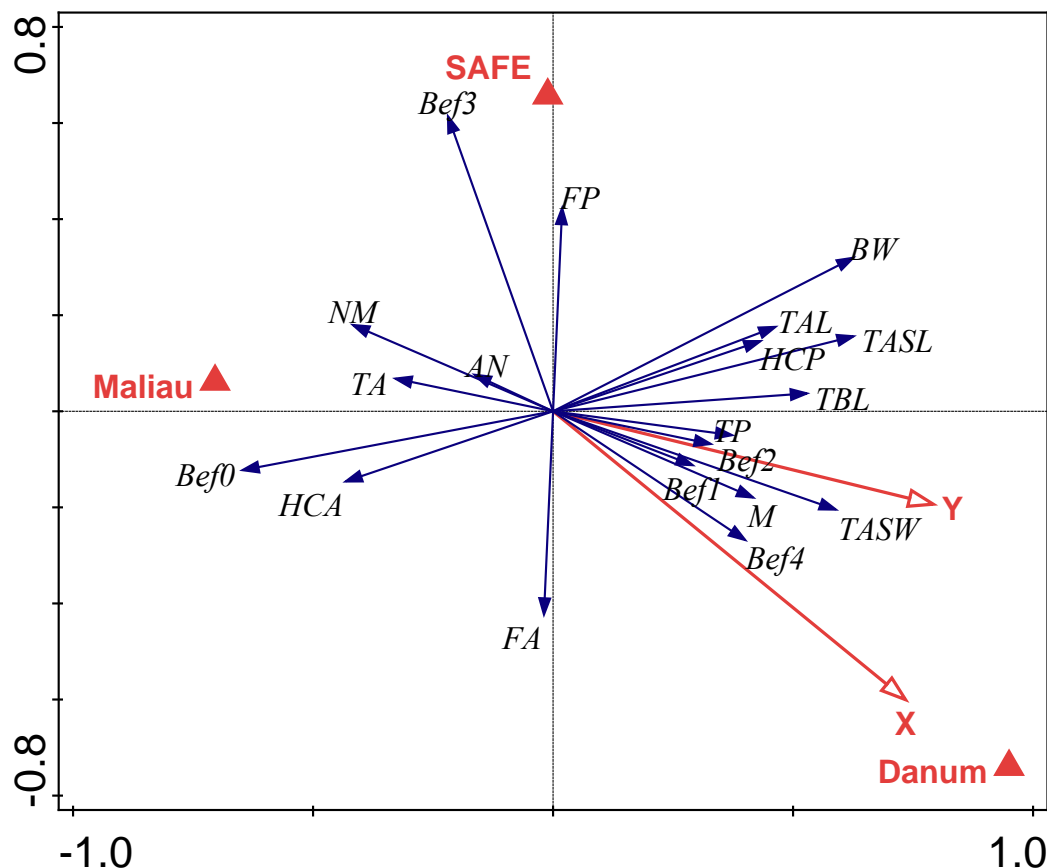
Fig. 4. Redundancy Analysis (RDA) ordination diagram of averaged Pselaphinae beetle functional traits (blue arrows) and environmental variables (red arrows, x-latitude and y-longitude). (TBL-body length, BW-body width, AL-antennal length, TASL-terminal antennal segment length, TASW- terminal antennal segment width, HCP-hollow cavity present, HCA-hollow cavity absent, TP-trichomes present, TA-trichomes absent, FP-foveae present, FA-foveae absent, Bef-basal eltryal foveae (0, 1, 2, 3, 4), M-myrmecophile, NM-non-myrmecophile).

Table 5. Statistical values obtained by RDA for averaged functional traits and environmental variables across all three sites.

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.1811	0.0610	0.0292	0.0072
Explained variation (cumulative)	18.11	24.21	27.13	27.85

Pselaphinae beetle functional diversity

Old growth rainforest sites Danum and Maliau recorded the highest ant abundances (7,759 and 7,287, respectively) and ant genus richness (176 and 231, respectively) compared with logged rainforest site SAFE (3,455 and 170). Pselaphinae beetle functional diversity (FD) is significantly associated with both ant abundances and ant genus richness across all three sites (Table 6). The presence of myrmecophile functional traits increases as both ant abundance and ant genus richness increases (Fig. 5).

(a)

(b)
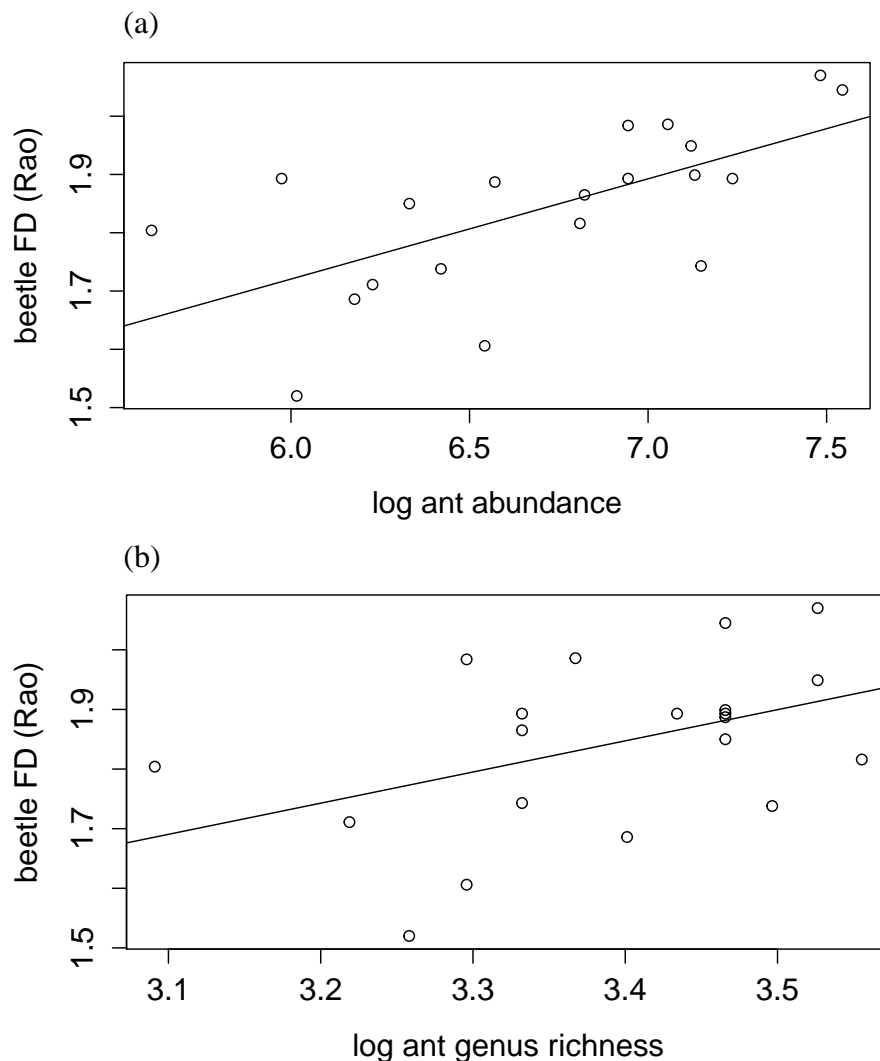
Fig. 5. The response of beetle functional diversity to (a) ant abundances and (b) ant genus richness across all threes sites.

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Table 6. Statistical values obtained by RDA for ant abundance and ant genus richness across all three sites (Danum, Maliau and SAFE).

| Predictor	Explained variance	F	P
Ant abundance	0.42	12.8	0.004
Ant genus richness	0.19	4.3	0.048

Beetle myrmecophile traits

In this study, 12 morphospecies belonging to 6 different tribes were assigned as probable myrmecophiles, from a total of 42 total morphospecies recorded (Fig. 6-8).
Two morphospecies were recorded from the tribe Clavigerini (Fig. 6A, B). Five morphospecies were recorded form the tribe Cyathigerini, distinctly characterized by their antennal club (Fig. 7). Only one morphospecies was recorded form the tribe Arnyllini, known for having almost symmetrical filiform antenna (Fig. 6C). Morphospecies recorded from the tribes Tmesiphorini (Fig. 46D, Fig. 8J), Tyrini (Fig.8L) and Batrisini (Fig. 8K), all exhibit moniliform antenna with enlarged terminal antennal segments.
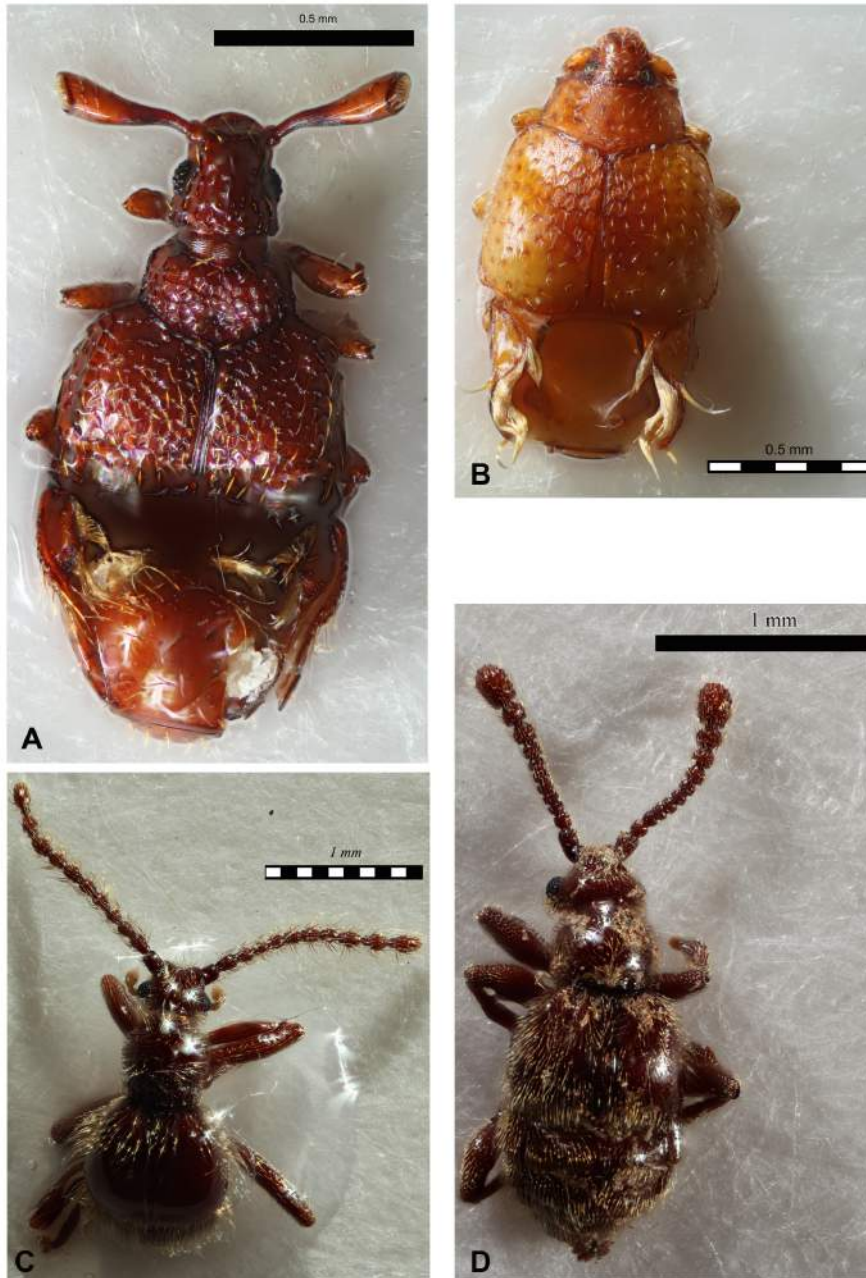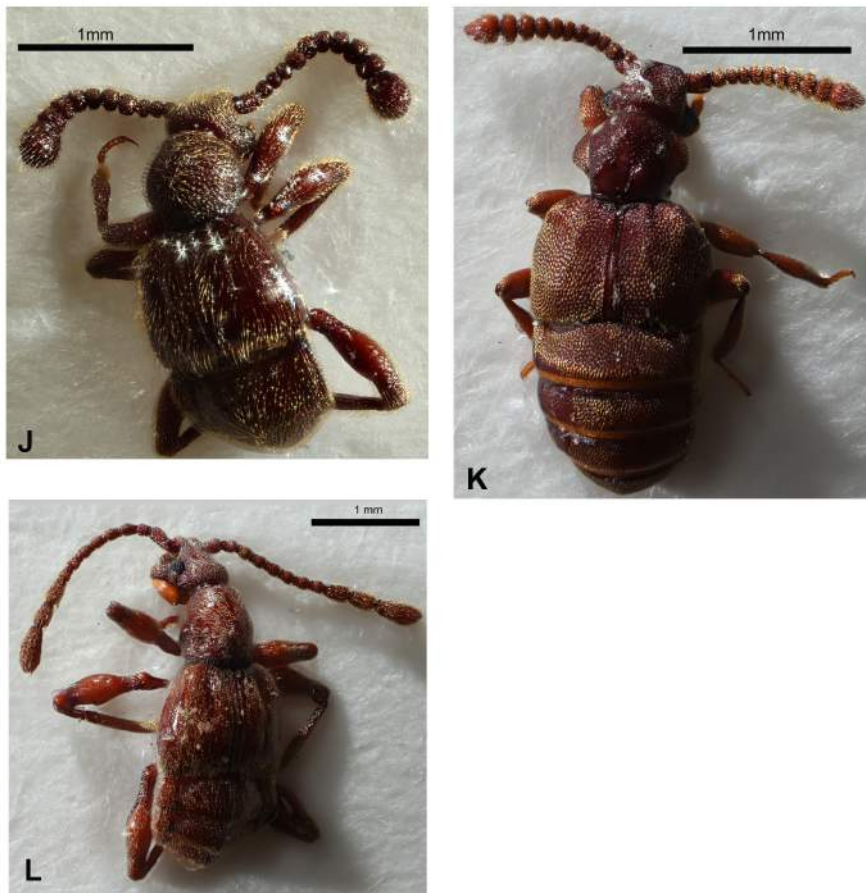
Fig. 6. Myrmecophile Pselaphinae beetles (A) morphospecies 1, (B) morphospecies PH, (C) morphospecies E (D) morphospecies 11. Magnification: A and B (x10), C and D (x4).
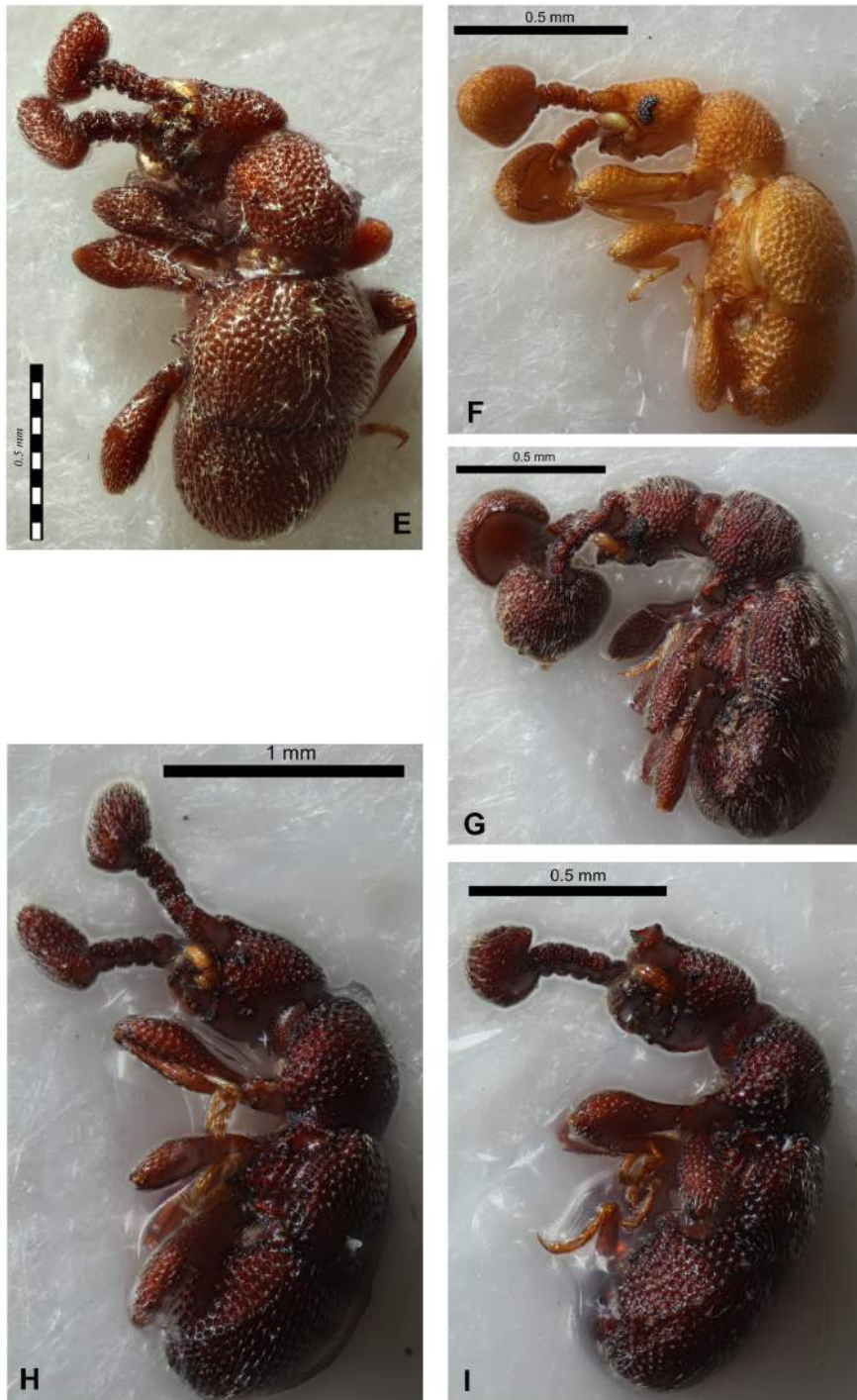
Fig. 7. Myrmecophile Pselaphinae beetles (E) morphospecies D, (F) morphospecies G, (G) morphospecies I, (H) morphospecies Z, (I) morphospecies W. Magnification: all images (x10).

Fig. 8. Myrmecophile Pselaphinae beetles (J) morphospecies F, (K) morphospecies 19, morphospecies T (L). Magnification: all images (x4).

Tribe Clavigerini

Obligate myrmecophiles belonging to the tribe Clavigerini (Fig. 9A, B) have a reduced number of antennal segments (3 segments, Fig. 9C), are sparsely pubescent and lack any foveae. They are also characterized by a large basal depression in the abdomen bearing large tufts of trichomes (Fig. 9D).

Tribe Cyathigerini

Morphospecies belonging to the tribe Cyathigerini (Fig. 10A-F, Fig. 11A, B) also have a reduced number of antennal segments (7 segments) and are characterized by unique antennal club structures. The antennal clubs of morphospecies D (Fig. 10B), W (Fig. 11A) and Z (Fig. 11B) are enlarged, highly pubescent block shaped terminal segments. In comparison, the antennal clubs of morphospecies G (Fig. 10E) and morphospecies I (Fig. 10F) are large and

round with the presence of a hollow cavity. Interestingly, trichomes are present inside the antennal club of morphospecies G (Fig. 10E) but are absent in morphospecies I (Fig. 10F). The morphospecies in the tribe Cyathigerini also exhibit a reduced number of foveae, lack the presence of trichomes (excluding morphospecies G, as mentioned previously) and are externally covered with impressions.

Tribe Tmesiphorini

Morphospecies 11 (Fig. 11E) and morphospecies F (Fig. 12A) both have a complete set of antennomeres (11 segments), which successively increase in size towards the terminal antennal segment and are highly pubescent across the entire body including the antenna. Both morphospecies exhibit a reduced number of bef, with only two sets of bef. Interestingly, morphospecies 11 lacks the presence of trichomes compared to morphospecies F. Trichomes are present in a circular structure along the metathoracic region (Fig. 12E) and are also present in a linear manner along the abdominal tergites. Antennal segments 6-11 of morphospecies F appear to have shallow cavities embedded with impressions and setae on the ventral side (Fig. 12C).

Tribe Tyrini

Morphospecies T (Fig. 11C) has a complete set of antennomeres (11 segments), with 9-11 enlarged. Morphospecies T is highly pubescent across the entire body including the antenna, lacks the presence of trichomes and has a reduced number of bef; two sets of bef.

Tribe Arnyllini

Morphospecies E (Fig. 11D) has a complete set of almost symmetrical antennomeres (11 segments), lacks the presence of trichomes although highly pubescent across the entire body, particularly along the antennae. Morphospecies E has a reduced number of bef; only one set of bef.

Tribe Batrisini

Morphospecies 19 (Fig. 12B) exhibits highly pubescent moniliform antenna (11 segments), which successively increase in size towards the terminal antennal segment. Morphospecies 19 also has a reduced number of bef; three sets of bef. Trichomes are present in small tufts emerging from large impression across the elytra (Fig. 12D, E), pronotum and abdomen of morphospecies 19.

*Non-myrmecophile beetles exhibiting myrmecophile traits*

Morphospecies 6 (Fig. 13A), morphospecies 12 (Fig. 13C) and morphospecies P (Fig. 13B) are not classified as probable myrmecophile Pselaphinae beetles. However, morphospecies 12 and morphospecies P both have trichomes and a reduced number of foveae. Morphospecies 6 lacks trichomes but is highly pubescent and has two sets of bef (Fig. 13A). Interestingly, antennal segments 6 and 7 of morphospecies 6 create a convex V-shape along the antennae, an antennal structure that has not been recorded in any other morphospecies in this study.
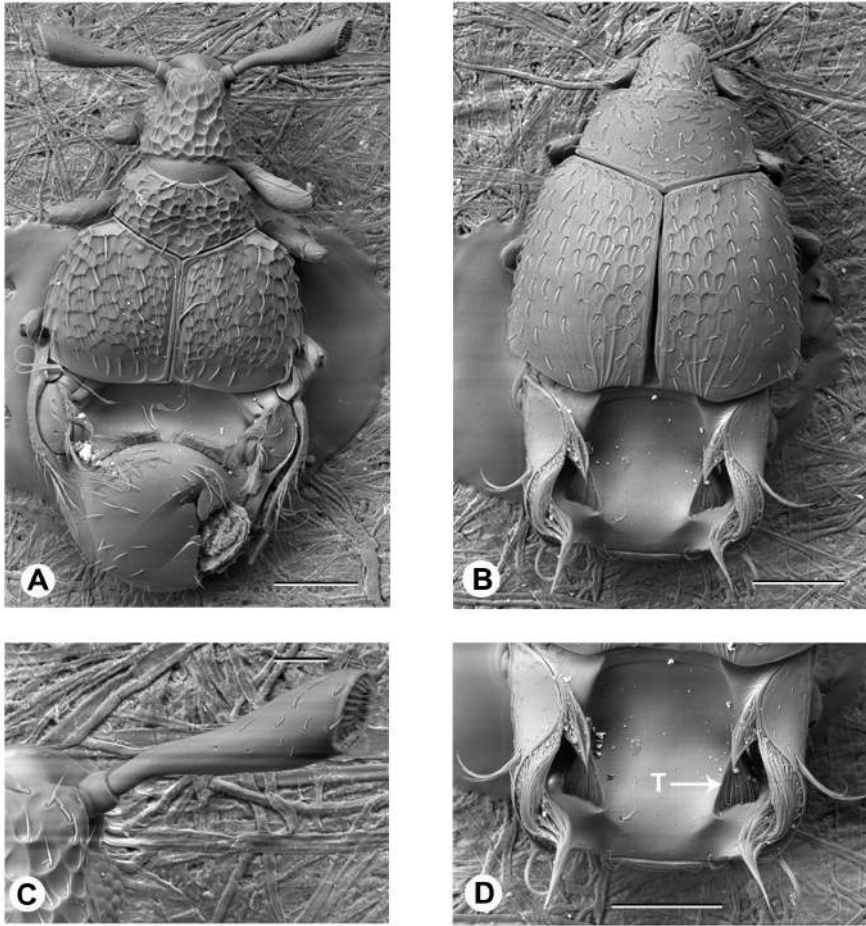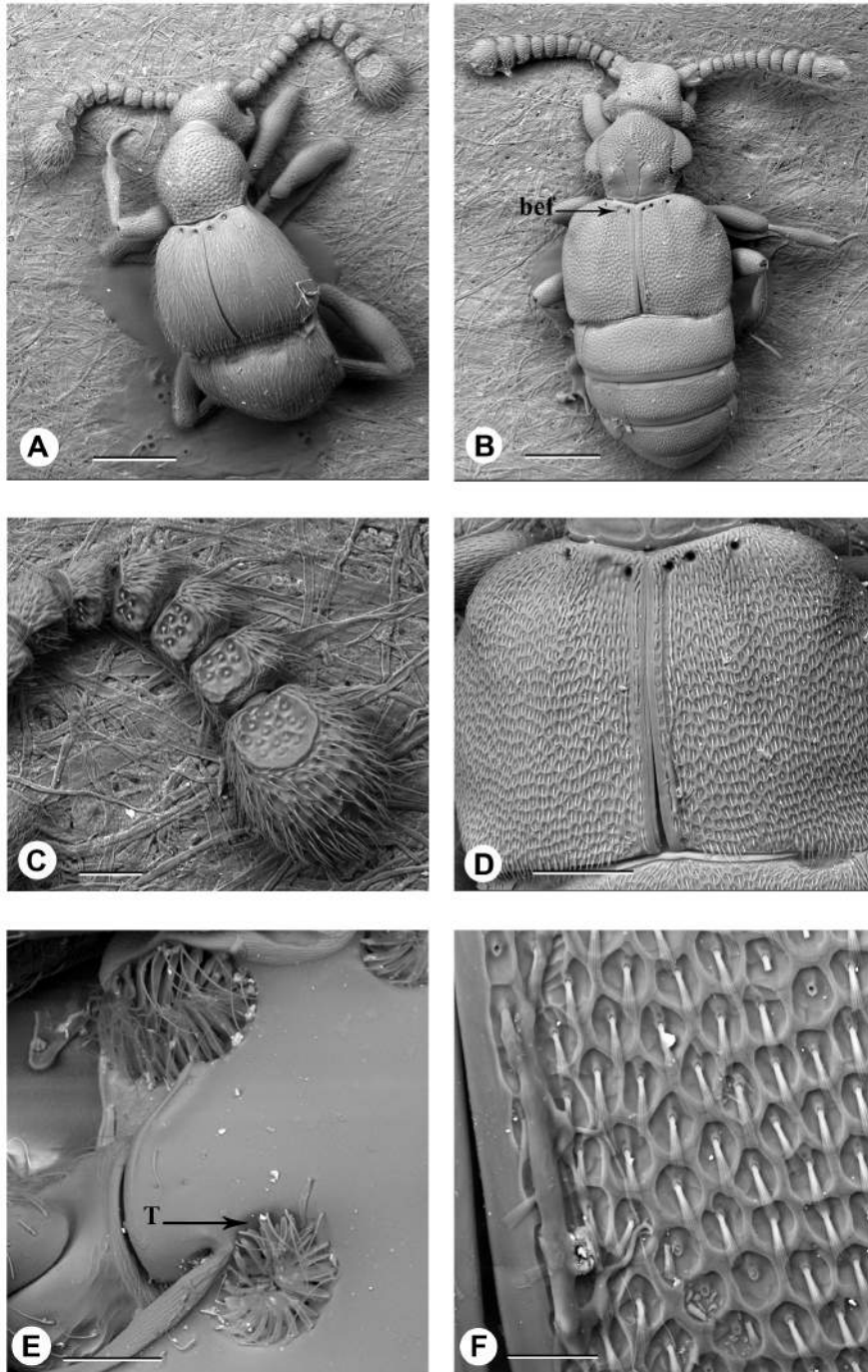
Fig. 9. Dorsal view SEM images of Pselaphinae tribe Clavigerini, (A) genus Cerylambus, (B) genus Pseudacerus, (C) Cerylambus antennae, (D) Pseudacerus abdomen, trichomes (T). Scale: A, B, D-200mm and C-60mm.
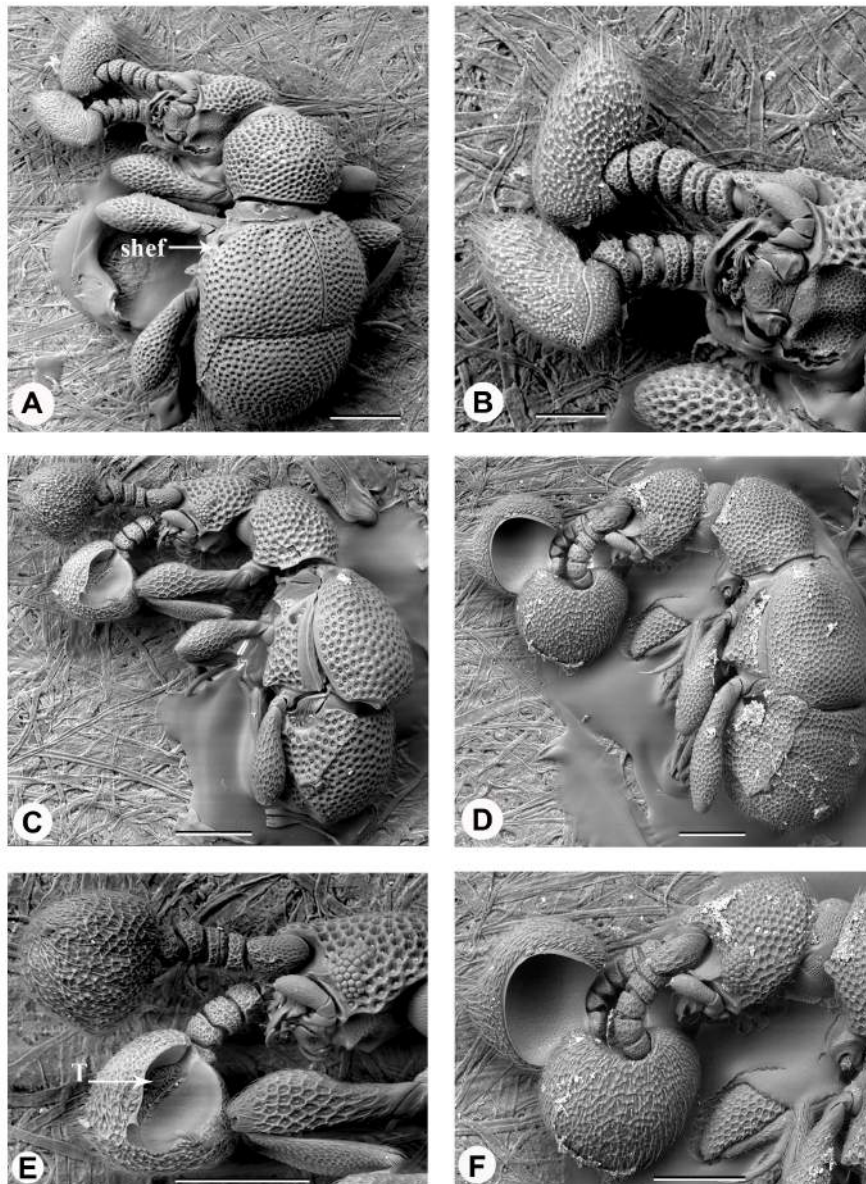
Fig. 10. SEM images of Pselaphinae tribe Cyathigerini genus *Plagiophorus*. (A) Dorsal view, morphospecies D, subhumeral elytral foveae (shef), (B) morphospecies D antennae, (C) side view, morphospecies G, (D) side view, morphospecies I, (E) morphospecies G antennae, trichomes (labeled T), (F) morphospecies I antennae. Scale: A, C, D, E, F-200mm and B-100mm.
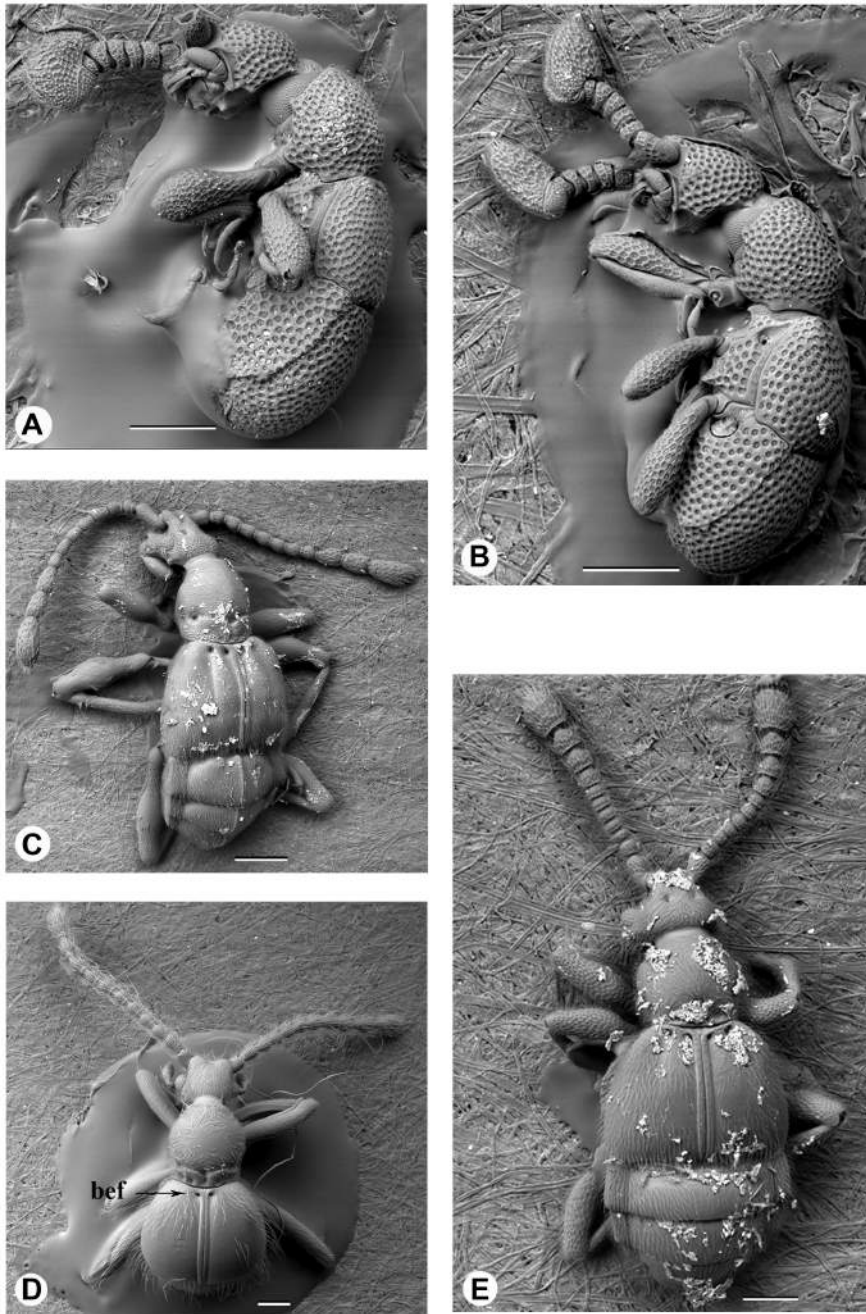
Fig. 11. (A and B) Side view SEM images of the Pselaphinae beetle tribe Cyathigerini genus Plagiophorus (A) morphospecies W, (B) morphospecies Z. (C) dorsal view, tribe Tyrini, morphospecies T, (D) dorsal view, tribe Arnyllini, morphospecies E (labeled bef), (F) dorsal view, tribe Tmesiphorini, morphospecies 11. Scale: A and C-400mm and B, D and E-200mm.

Fig. 12. Dorsal view SEM images of Pselaphinae beetle tribe (A) Tmesiphorini genus Pseudophanias, morphospecies F and (B) Batrisini genus Diagus, morphospecies 19, basal elytral foveae (bef). (C) morphospecies F antennae (D) morphospecies 19 elytra (E) morphospecies F abdominal trichomes (T), (F) morphospecies 19 elytral trichomes. Scale: A and B-400mm, C-100mm, D-200mm, E-60mm and F-40mm.
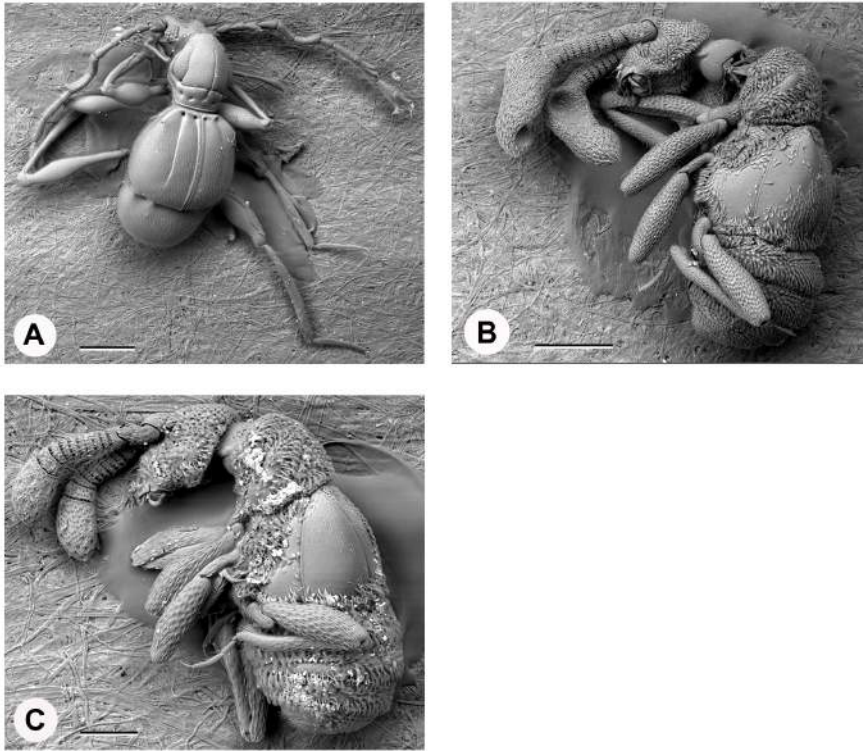
Fig. 13. SEM images of Pselaphinae beetle (A) tribe Batrisini genus Cratna, morphospecies 6, dorsal view (B) tribe Hybocephalini genus Apharinodes, morphospecies P, side view (C) tribe Hybocephalini genus Apharinodes, morphospecies 12, side view. Scale: A and B-400mm and C-200mm.

Discussion

The composition of leaf litter Pselaphinae beetles, inhabiting tropical rainforests of Sabah, Borneo, is strongly associated with environmental conditions at a site level, thus supporting the first hypothesis. Myrmecophile functional traits were strongly associated with site environmental conditions and associated with Pselaphinae beetle community composition, which supports the second hypothesis. Ant diversity (ant abundance and genus richness) appears to be a possible driver of Pselaphinae beetle functional diversity. Pselaphinae beetle composition varied not only between logged (SAFE) and old growth (Danum and Maliau) rainforest sites but interestingly between the two old growth rainforests sites as well. Functional diversity of Pselaphinae beetles increased as ant abundance and genus richness increased, thus supporting the third hypothesis.

Pselaphinae beetle community composition

The differences in Pselaphinae beetle composition observed between logged (SAFE) and old growth (Danum and Maliau) rainforest sites is to be expected given the difference in landscape structure. Sample plots located within SAFE have all been twice logged (Ewers *et al.,* 2011), greatly reducing canopy cover, altering leaf litter composition and exposing the rainforest floor, due to a shift from old growth to regenerating vegetation. Habitat quality and floral diversity in tropical rainforests have been shown to be significantly associated with leaf litter invertebrate biodiversity (Barton *et al.,* 2010; Donoso *et al.,* 2013), which in turn provides important ecosystem services, contributing to habitat quality (Ebeling *et al.,* 2014). Ottermanns *et al.* (2011) reported that changes in vegetation composition results in varying structural characteristics of leaf litter, which in turn can alter the microclimatic conditions within the leaf litter. Subsequently, these changes strongly influence the leaf litter beetle community (Ottermanns *et al.,* 2011). Vasconcelos and Laurance (2005) demonstrated that changes in plant species composition as a result of land cover changes in the Amazonian rainforest, affect decomposition, which in turn affect leaf litter quality. Leaf- litter decomposition is directly determined by the structural characteristics and nutrient content of the leaves and therefore intimately associated with leaf litter quality (Sundarapandian & Swamy, 1999). A study by Sackchoowong *et al.* (2008) revealed that Pselaphinae beetle assemblages were significantly associated with two important microenvironmental variables: leaf litter and soil moisture. Interestingly, temperature, canopy cover and soil moisture were

not significantly associated with Pselaphinae beetle composition across any of the three sites in the current study. Microenvironmental variables such as leaf litter mass and leaf litter depth were not measured in the current study, however, and should be considered in future studies as they may potentially provide a better understanding of the habitat-specific requirements of Pselaphinae beetles.

Comparisons of Pselaphinae beetle composition between two old growth rainforest sites

Diptocarpaceae and Euphorbiaceae tree families dominate lowland dipterocarp rainforests across Borneo (Slik *et al.,* 2003). However, Floral diversity of lowland dipterocarp rainforests varies strongly at a local scale and geographical distances have been significantly associated with changes in floristic diversity (Slik *et al.,* 2003). Danum Valley and the Maliau Basin Conservation Areas are geographically situated 100 km apart and although are both classified as old growth rainforests, differences in their vegetation structure have been recorded (Benedick *et al.,* 2006). Trees in the family Euphorbiaceae are a predominantly understory tree family that dominates Danum Valley Conservation Area, which consists of fewer large trees, thus creating a lower frequency of small near-ground canopy gaps (Newbery *et al.,* 1992). This supports the findings by Benedick *et al.* (2006), which reported higher mean tree heights and canopy cover in the Maliau Basin compared with Danum Valley. Furthermore, Danum Valley recorded higher ground vegetation cover compared with the Maliau Basin (Benedick *et al.,* 2006). Differences in Pselaphinae beetle composition recorded between Danum and Maliau could therefore be due to the variability of vegetation at small spatial scales, creating differences in microclimatic conditions. In a study by Luke *et al.,* (2014) functional group composition of ants was strongly associated with habitat quality and leaf litter cover. This supports the finding by Bastos and Harada (2011), which revealed leaf litter availability and thus habitat quality positively influenced ant species richness, in primary Amazonian rainforest sites. The leaf litter microhabitat differences between Danum and Maliau could therefore influence ant community compositions, which in turn will impact on myrmecophile Pselaphinae beetle composition. This was evident from the results recorded in the current study, which revealed probable myrmecophile Pselaphinae beetle composition varied between Danum and Maliau. Morphospecies E belonging to the tribe Arnyllini was equally abundant in both Maliau and Danum, however morphospecies 19 belonging to the tribe Batrisini was only present in Maliau. Morphospecies T belonging to the tribe Tyrini also showed a preference for Maliau,

with lower abundances recorded in Danum. Obligate myrmecophile morphospecies PH belonging to the tribe Clavigerini was only present in Danum in comparison with morphospecies 1 also belonging to the tribe Clavigerini that was recorded in all three sites. Morphospecies F belonging to the tribe Tmesiphorini was the most numerically dominant probable myrmecophile Pselaphinae beetle recorded and although recorded across all three sites, high abundance of morphospecies F was recorded in Danum. In comparison, morphospecies 11 also belonging to the tribe Tmesiphorini was not recorded in Danum but high abundance was recorded in Maliau.

Functional traits and probable myrmecophile Pselaphinae beetle composition

The diversity of vegetation and high quality microhabitats in undisturbed primary rainforest sites Danum and Maliau support high abundances and genus richness of leaf litter ants which is associated with high abundance of probable myrmecophile Pselaphinae beetles. In particular, myrmecophile functional traits of Pselaphinae beetles were strongly associated with Danum Valley including body length, reduced number of foveae and the presence of trichomes. These results agree with the morphological features that are characteristic of a myrmecophile Pselaphinae beetle (Parker & Maruyama, 2013; Yin & Li 2013; Chandler, 2001). Furthermore, myrmecophile Staphylinidae beetles have been described as having apically widened antenna (Maruyama *et al.,* 2014), which supports the findings that terminal antennal segment width is also strongly associated with probable myrmecophily, reported in the current study. The arrangement and presence or loss of Foveae has been recognized as one of the most important morphological structures for taxonomic identification of Pselaphinae beetles (Park, 1942; Chandler, 2001). The functional role of foveae remains unknown, however, two probable foveal functions have been proposed by Chandler (2001); 1) thoracic foveae are utilized for a sensory function and 2) abdominal and head foveae provide structural rigidity. Moreover, the evolutionary trend of foveae appears to be towards loss with primitive Pselaphinae beetles exhibiting a more diverse set of foveal patterns across the entire body (Chandler, 2001). Although the functional role of foveae is unrelated to myrmecophily, there is an evolutionary trend towards loss with ant-associated Pselaphinae beetles, specifically with regards to the basal elytral foveae sets (Chandler, 2001; Parker & Maruyama, 2013). This is evident form the results obtained in the current study, whereby morphospecies R and 8 recorded from the tribe Proterini retain a complete set of basal elytral foveae and have not been classified as probable myrmecophiles. Probable myrmecophile

Pselaphinae morphospecies recorded in the tribes Tmesiphorini and Tyrini all exhibit a reduction of two sets of basal elytral foveae and tribes Arnyllini and Cyathigerini retain just one set of basal elytral foveae. Obligate myrmecophile Pselaphinae morphospecies 1 and PH belonging to the tribe Clavigerini show a complete loss in basal elytral foveae.

Interestingly, the tribe Cyathigerini comprising five probable myrmecophile morphospecies was dominant in the logged (SAFE) rainforest sites. The distinctively clubbed terminal antennal segments are suggestive of morphological structures that may be associated with myrmecophily, in that they potentially provide structures for worker ants to hold onto while transporting the beetle into the ant's nest. I hypothesize, that due to their numerical dominance in the logged rainforests site (SAFE) with lower ant diversity, their unique antennal clubs may not be directly associated with myrmecophily, although they form a facultative association with ants (Sugaya *et al.,* 2004). Male *Plagiophorus species* in the tribe Cyathigerini, recorded from Borneo have enlarged round antennal clubs (Nomura & Mohamed, 2008) exhibited by morphospecies G and I. One female *Plagiophorus species* has been recorded from Borneo that has a block-like antennal club (Nomura & Mohamed, 2008) exhibited by morphospecies D and Z. I speculate such unique morphological structures to be associated with sexual dimorphism and may play an essential role in beetle copulation. The genus Cyathigerini has been documented for exhibiting remarkable sexual dimorphism in the antennal club and has been suggested that the female block-like antennal club inserts inside the excavated male antennal club, during copulation (Sugaya *et al.,* 2004). However, behavioural information on mating in Pselaphinae beetles largely remains unknown and absent from the literature. Furthermore, the presence of trichomes inside the antennal club of morphospecies G and the absence of trichomes in morphospecies I lead to further speculation about the functional role of such unique structures. I speculate that the presence of trichomes in morphospecies G is not associated with ants, but a form of sexual dimorphism, and potentially species variation within this particular genus.

All members of the tribe Clavigerini are believed to be obligate myrmecophiles and are completely dependent on their ant hosts (Chandler, 2001; Park, 1942). Both morphospecies recorded in the current study exhibit reduced mouthparts for trophallaxis (Parker & Grimaldi, 2014; Park, 1942), a reduction and compaction of antenna and abdominal segments that supports the beetle when handled by ant workers and provides a larger surface area for glandular secretions to spread (Parker & Grimaldi, 2014; Cammaerts, 1992), and long tufts of trichomes that ornament the base of the abdomen providing an important functional role during trophallaxis feeding by ant workers and social integration

inside the ant colonies (Parker & Grimaldi, 2014; Cammaerts, 1992). Trichomes facilitate the dispersion of secretions produced by secretory Wasmann glands that are both attractive to and consumed by the ants thus initiating trophallaxis by the ant to the beetle (Hill *et al.,* 1976; Parker & Grimaldi, 2014). Although trichomes appear to play an important functional role in the symbiotic association between ants and beetles, it cannot always be assumed that the presence of trichomes defines a myrmecophile. Morphospecies P and 12 belonging to the tribe Hybocelaphini, recorded in the current study, both exhibit compact antenna and are densely covered with trichomes, however, they have not been classified as probable myrmecophile Pselaphinae beetles. Morphospecies 6 belonging to the tribe Batrisini, recorded in the current study, although lacks the obvious functional traits associated with myrmecophily (as previously discussed) exhibits a unique morphological antennal modification, whereby antennomere six and seven create a convex V-shape. Although the functional role of such a unique antennal modification remains unknown, it may acts as a 'handle' to aid ant workers during transport of the beetle inside the ant nest, if at all this particular Pselaphinae morphospecies forms any association with ants. There are very few if any, behavioral studies carried out on Pselaphinae beetles, given the difficulty in their small size and microhabitat, therefore it is difficult to conclude whether or not morphospecies P, 12 and 6 form any association with ants. It therefore it is vital that behavioural studies on Pselaphinae beetles are carried out in order to complement morphological studies and provide a better understanding for future ecological studies.

Pselaphinae beetle community composition is associated with site environmental conditions. However, the degree to which myrmecophile Pselaphinae beetles community composition varies across the three sites (Danum, Maliau and SAFE) requires further investigation and measurement of important microenvironmental variables, such as leaf litter depth and mass, which evidently were not measured in the original fieldwork. Morphometric analysis on leaf litter Pselaphinae beetles sampled in the current study, hopefully, provide further knowledge into the possible functional roles and ecological interactions Pselaphinae beetles exhibit within the dynamic microhabitat of the rainforest floor. Ant diversity appears to be a possible driver of Pselaphinae beetle functional diversity and therefore it is plausible to predict that there will be loss of probable myrmecophile Pselaphinae beetles after the ant suppression treatments have taken place. This study provides evidence of the threats land-cover changes could potentially have on ecosystem functioning, impacting the biodiversity of Malaysian Borneo.

Acknowledgements

I would like to say a big thank you to my project supervisor Dr. Paul Eggleton, for his continuous support and guidance throughout the duration of this project and for making it such an invaluable and enjoyable experience. I would also like to say thank you to Sholto Holdsworth for his support and invaluable discussions on Pselaphinae beetles. Thank you to Coleopterist Roger booth and Peter M Hammond who took time to examine my specimens and share their profound knowledge on the Pselaphinae beetles. I would like to say a big thank you to Coleopterist Joseph Parker for his taxonomic identification of all morphospecies recorded, for which I am extremely grateful. I would also like to say thank you to Alex Ball for providing training on scanning electron microscopy and his support and guidance throughout the imaging process. Thomas Bell for providing me with the relevant ant data for this project and for being a supportive friend throughout this project. Thank you to the volunteers of the Soil Biodiversity Group for sorting out the specimens, prior to this study.

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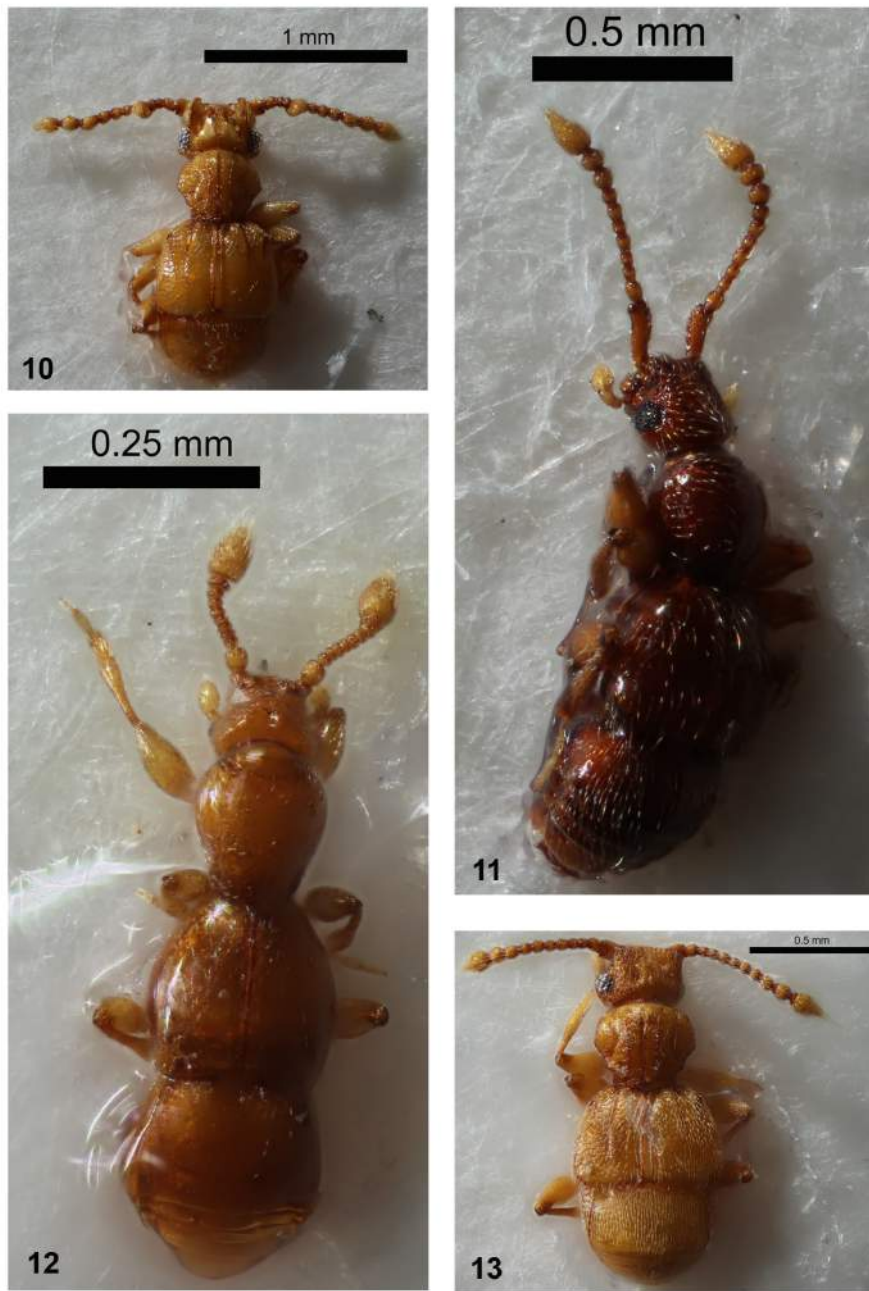
Appendix
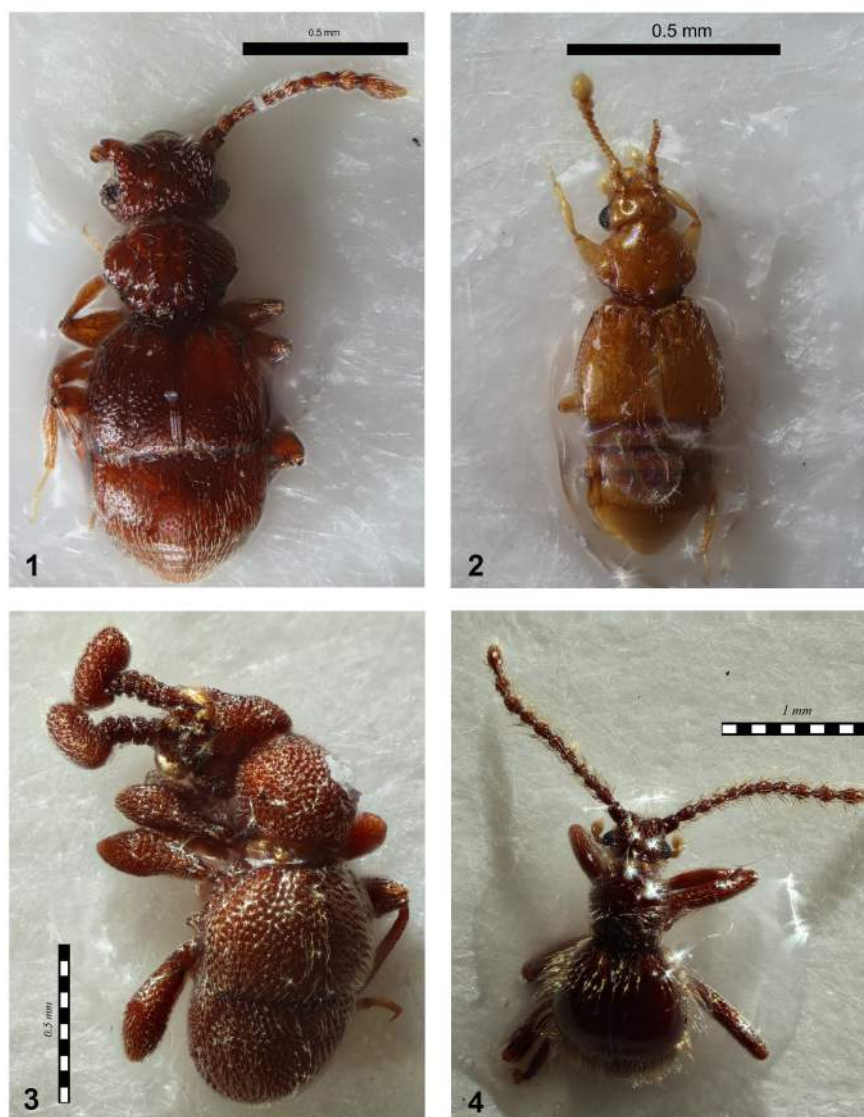
Fig. 1. (1) morphospecies A, (2) morphospecies C, (3) morphospecies D and (4) morphospecies E.
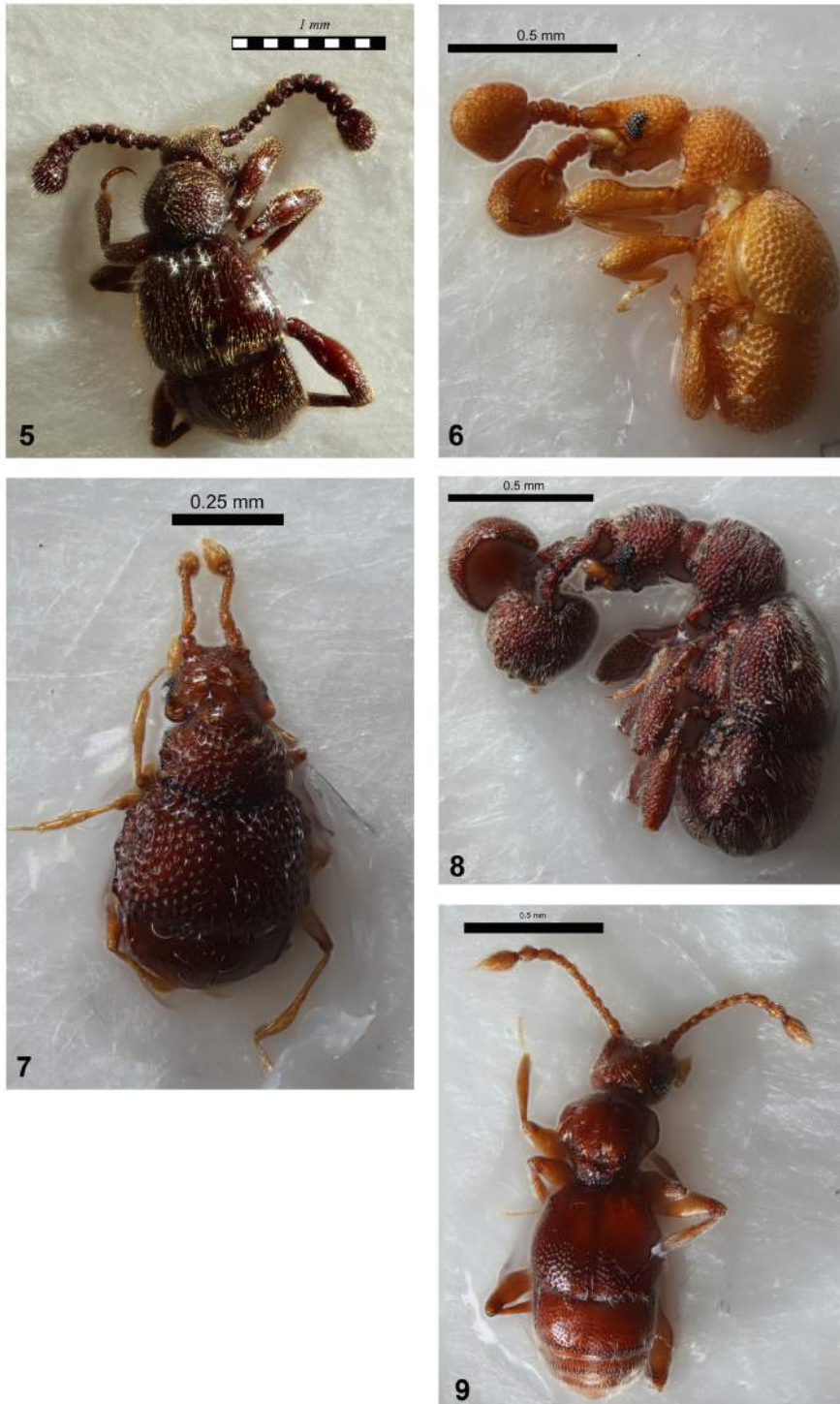
Fig. 2. (5) morphospecies F, (6) morphospecies G, (7) morphospecies H, (8) morphospecies I and (9) morphospecies J.

Fig. 3. (10) morphospecies L, (11) morphospecies N, (12) morphospecies O and (13) morphospecies Q.

Fig. 4. (14) morphospecies R, (15) morphospecies S, (16) morphospecies T and (17) morphospecies U.

Fig. 5. (18) morphospecies V, (19) morphospecies W, (20) morphospecies Y and (21) morphospecies Z.
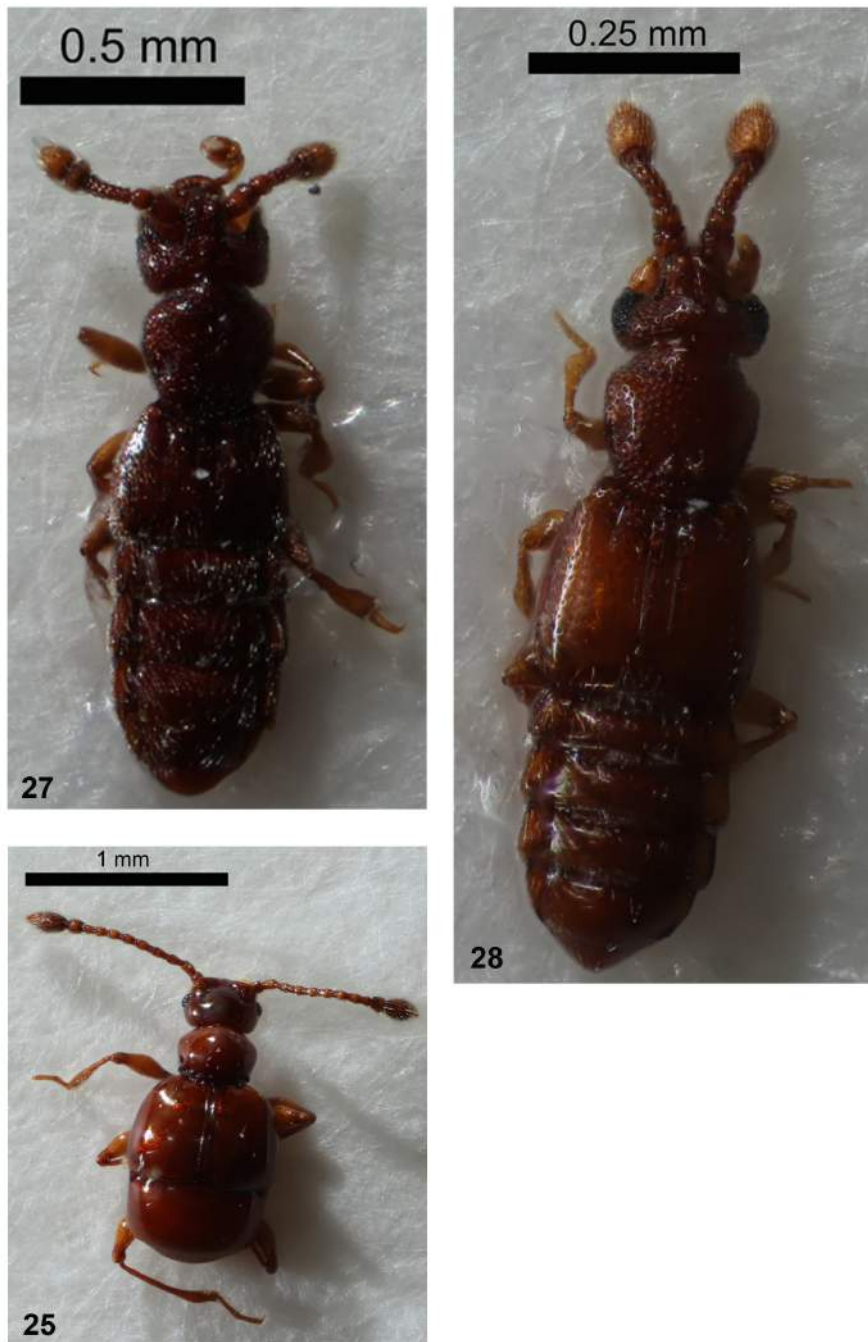
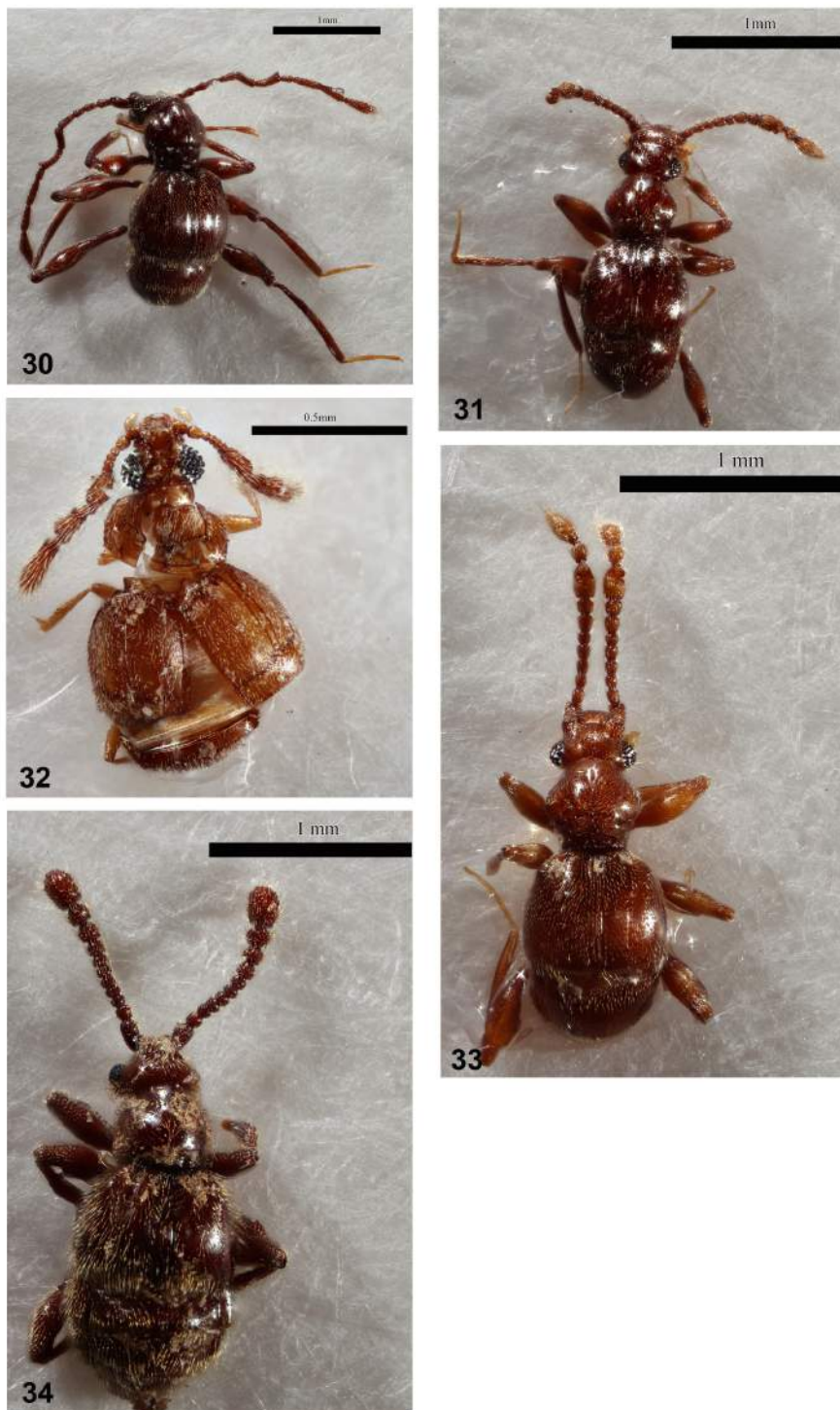**Fig. 6.** (22) morphospecies AA, (23) morphospecies AC and (24) morphospecies PH.

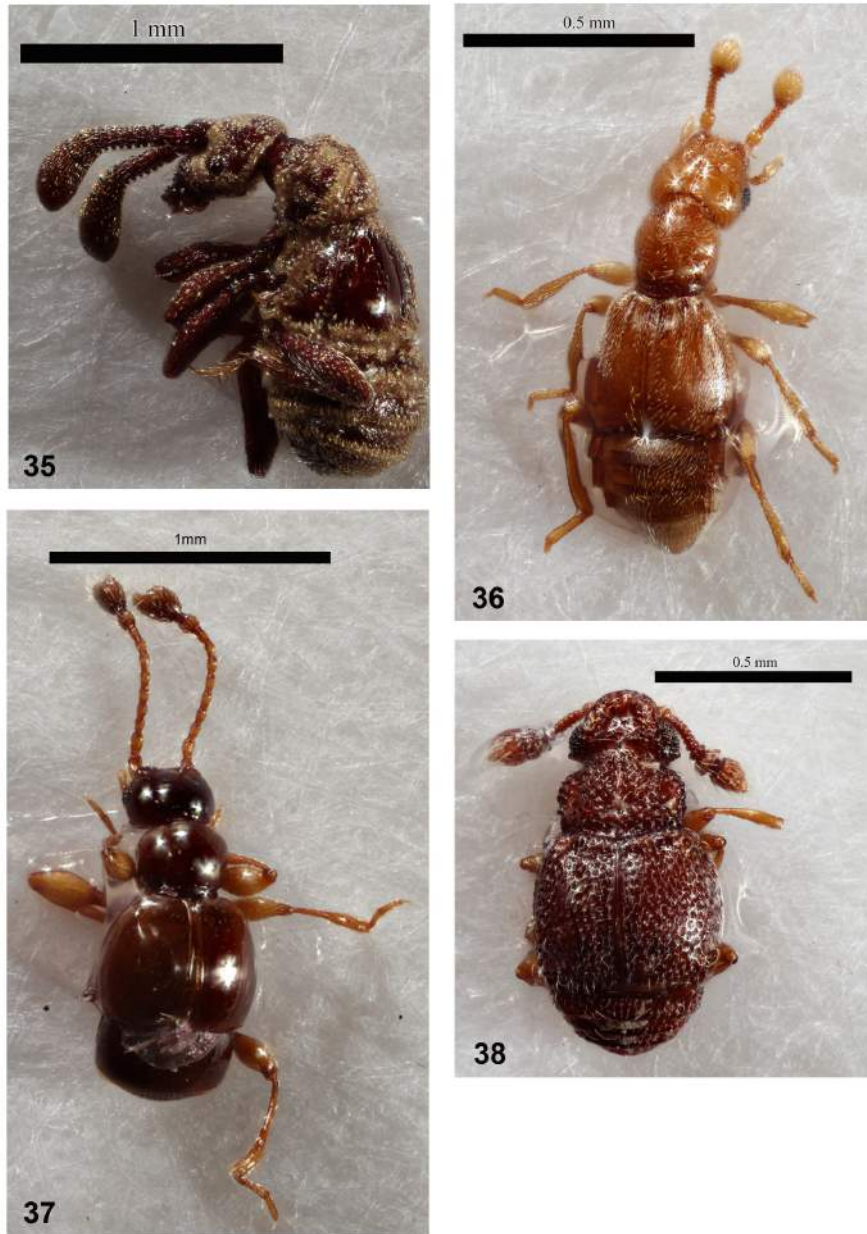**Fig. 7.** (25) morphospecies 1 and (26) morphospecies 2.

Fig. 8. (27) morphospecies 3, (28) morphospecies 4 and ('25'-29) morphospecies 5.

Fig. 9. (30) morphospecies 6, (31) morphospecies 7, (32) morphospecies 8, (33) morphospecies 9 and (34) morphospecies 11.

Fig. 10. (35) morphospecies 12, (36) morphospecies 13, (37) morphospecies 15 and (38) morphospecies 17.

Fig. 11. (39) morphospecies 18, (40) morphospecies 19, (41) morphospecies AB and (42) morphospecies P.