

A list of ants from Lambir Hills National Park and its vicinity, with their biological information:

Part II. Subfamilies Leptanillinae, Proceratiinae, Amblyoponinae, Ponerinae, Dorylinae, Dolichoderinae, Ectatomminae and Formicinae

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ABSTRACT A list of ants of the subfamilies Leptanillinae, Proceratiinae, Amblyoponinae, Ponerinae, Dorylinae, Dolichoderinae, Ectatomminae and Formicinae from Lambir Hills National Park, Sarawak, Borneo is presented with biological information. In this report 347 species in 61 genera are recorded, with 10 species newly recorded from Borneo. Literature treating species of the above-mentioned subfamilies from Lambir Hills National Park is listed. In total (Part I & II), 579 species in 96 genera are recorded from this national park, representing the largest species number so far known in one place in Asia. Among the 579 species only 53% (307) are identified to species, the others no doubt including many species new to Borneo or even to science.

KEY WORDS ant-mimicking spider / biology / Borneo / collection data / dipterocarp forest / extrafloral nectary / Formicidae / honeydew / homopteran / named species / nesting site / new record / Sarawak / sugar/honey bait / Southeast Asian tropical rainforests / taxonomic notes / total number of species

Introduction

In this second part we will treat all the subfamilies that were not treated in the first part (Yamane et al. 2018a). Data source is mostly same as that in the first part. The total number of species listed in both parts is presented for each genus and subfamily. Features characterizing the ant fauna of Lambir Hills National Park are discussed focusing on the lack/paucity and dominance of particular species/groups. The faunal composition in Lambir is compared with those in other sites in Southeast Asia that have been intensively surveyed such as Bogor Botanical Garden (Ito et al. 2001), Pasoh Forest Reserve (Malsch et al. 2003, Fiala & Guan 2003), etc.

Survey sites and methods

Collection sites

Ants were sampled in Lambir Hills National Park and its close vicinity, Miri, Sarawak, East Malaysia (Borneo). Most samples were collected in areas around the head quarter, mainly in the 8 ha plot and canopy 4 ha that are covered with primary forests. For further information on Lambir Hills National Park and our collecting sites, see Inoue & Hamid (1997), Hazebroek & Abang Kashim (2006) and Part I of this paper (Yamane et al. 2018a).

Collection methods

Ants were collected manually with forceps or aspirators by searching ground surface (decayed wood, under stones, leaf litter etc.), lower vegetation (tree trunks close to ground surface, forest floor plants, foliage of trees etc.), and higher levels of trees from the tree towers, walkways and canopy crane, and by directly climbing trees. Ground-level ant fauna was also studied using honey (sugar) baits; arboreal ants were net-swept or with baiting to compare ant species composition between different sites. Biological information was got mainly by colony collection, baiting and direct observations (see below). ‘Ant-mimic samples’ derived from the sampling of ants in the ‘Ant-mimic spiders’ program by Y. Hashimoto and others, and are not necessarily involved in direct mimic-model relationships. Numerous wet specimens (mainly winged ants) sampled by light trapping have not yet been identified.

Identification and arrangements of species

Identification at genus level was mainly made by consulting Bolton (1994). A comprehensive classification system of Formicidae was given by Bolton (2003). However, during recent years new taxonomic systems of ants have been proposed principally based on DNA phylogenies (Boudinot 2015 for entire Formicidae; Brady et al. 2014 for Dorylinae; Schmidt & Shattuck 2014 for Ponerinae; Ward et al. 2016 for Formicinae).

Species are listed alphabetically for each genus, or for each subgenus or species-group in the genera having more than one subgenus or species group. Species entries also include those with ‘cf. names’ like *Hypoponera* cf. *mesoponeroides* (Radchenko 1993), although they are counted as unidentified species in statistics. SKY species codes, when available, are given in parentheses following species names. Unidentified species without ‘cf. names’ are listed by SKY species codes at the end of each genus, subgenus or species group. Each of the species newly recorded from Borneo is indicated by an asterisk (*); many of unidentified species might be new to Borneo or even new to science. In cases where detailed location data are not available on data labels, the collection site is simply described as ‘Lambir’.

Sources of biological data

Information written on data labels of specimens and in Sk. Yamane's and H.O. Tanaka's field notebooks is mainly used. Unpublished data are occasionally cited for species observed/found on trees (H.O. Tanaka), in the transects for soil CO₂ emission study (M. Ohashi group), and for those net-swept at different strata of dipterocarp forests in 'ant-mimicking-spiders' project (Y. Hashimoto group), and those found to be attracted to *Endospermum* extra-floral nectaries observed by Sk. Yamane and H.O. Tanaka. Some papers dealing with ants observed in Lambir also contain biological information. Forest strata (ground level, lower vegetation, arboreal, canopy) cited in 'Biology' subsection denote the main vertical zones where the worker activity was seen; this does not necessarily mean that nesting was observed there.

Abbreviations

The following abbreviations are used in the list and figure captions. Sexes and castes: w, worker; fq, dealate queen (mostly founding queen); wq, winged queen; m, male. Collection sites: Bt., Bukit (hill); HQ, the headquarters. Collectors: HOT, H.O. Tanaka; SKY, Sk. Yamane. Others: EFN, extrafloral nectary.

**List of ants of the subfamilies Leptanillinae, Proceratiinae,
Amblyoponinae, Ponerinae, Dorylinae,
Dolichoderinae, Ectatomminae and Formicinae**

Subfamily Leptanillinae

Up to now two named species in two genera, *Anomalomyrma* and *Protanilla*, have been recorded from Borneo (Pfeiffer et al. 2011; *Leptanilla* material is stored in AntBase.Net Collection, University of Ulm, but not identified yet at species level). SKY collection contains worker specimens of unidentified *Leptanilla* species from East Kalimantan, Sabah and Sarawak. We have recognized one species belonging to *Protanilla* in Lambir Hills National Park.

Tribe Anomalomyrmini Taylor, 1990*Genus Protanilla* Taylor, 1990

Named Bornean species: 1 (Pfeiffer et al. 2011). Lambir species: 1 (named).

Protanilla rafflesi Taylor, 1990 (sp. 1 of SKY)

Collection data. 8 ha plot: w, fq & wq, 22.i.1993, SKY.

Biology. Forest; ground level.

Subfamily Proceratiinae

All the known extant genera of this subfamily are recorded from Lambir Hills National Park.

Tribe Probolomyrmicini Perrault, 2000

Genus *Probolomyrmex* Mayr, 1901

Named Bornean species: 3 (Eguchi et al. 2006, Pfeiffer et al. 2011). Lambir species: 3 (named) including one new to Borneo. Bolton (2003) assigned this genus to the tribe Proceratiini.

**Probolomyrmex dammermani* Wheeler, 1928 (sp. 1 of SKY)

Collection data. ‘Lambir’: w, 7.xi.2008, M. Yoshima (W1-L13/YM1233).

Biology. Forest; ground level.

Probolomyrmex itoi Eguchi, Yoshimura et Yamane, 2006 (sp. 2 of SKY)

Collection data. ‘Lambir’: w, 23.vi.1998, K. Eguchi.

Biology. Forest; ground level.

Literature. Eguchi et al. (2006).

Probolomyrmex maryatiaae Eguchi, Yoshimura et Yamane, 2006 (sp. 4 of SKY)

Collection data. 8 ha plot: w, 15.i.1993, SKY; w, 1.vii.1997, SKY.

Biology. Forest; ground level.

Literature. Yamane & Nona (1994; as *P. dammermani*), Eguchi et al. (2006).

Tribe Proceratiini Emery, 1895

Genus *Discothyrea* Roger, 1863

Named Bornean species: 0 (Pfeiffer et al. 2011, only genus recorded). Lambir species 3 (not identified to species). All species were collected at ground level in the forest.

Unidentified species in *Discothyrea*: **sp. 1 of SKY** (8 ha plot), **sp. 2 of SKY** (‘Lambir’: nest in soil), and **sp. cf. 3 of SKY** (‘Lambir’: 67-L13/YM-0500).

Genus *Proceratium* Roger, 1863

Named Bornean species: 10 (Baroni Urbani & de Andrade 2003, Pfeiffer et al. 2011). Lambir species: 3 (1 named, 2 unidentified). Baroni Urbani & de Andrade (2003) recorded five species from Sarawak.

Proceratium deelemani Perrault 1981 (sp. 3 of SKY)

Collection data. ‘Lambir’: w, 8.x.2008, M. Yoshima (80-L20/YM-0872).

Unidentified species in *Proceratium*: **sp. 13 of SKY** ('Lambir': 51-L20/YM0088: ex soil), and **sp. 14 of SKY** ('Lambir': ex soil).

Subfamily Amblyoponinae

Among the five Asian genera of this subfamily, *Xymmer* Santschi, 1914 has been known only from Vietnam (Satria et al. 2016). Pfeiffer et al. (2011) recorded four species in four genera from Borneo. We have collected five species in four genera from Lambir.

Genus *Myopopone* Roger, 1861

Named Bornean species: 1 (Pfeiffer et al. 2011). Lambir species: 1 (named).

Myopopone castanea (F. Smith, 1860) (sp. 1 of SKY)

Collection data. 8 ha plot: wq, 10.xii.1993, SKY.

Biology. The winged queen was collected during the daytime on the forest floor.

Genus *Mystrium* Roger, 1862

Named Bornean species: 1 (Pfeiffer et al. 2011). Lambir species: 1 (named).

Mystrium camillae Emery, 1889 (sp. 1 of SKY)

Collection data. 8 ha plot: w, 17.viii.1997, SKY. Bt. Pantu: w, 16.i.1993, SKY. 'Lambir': w, 14.i.2012, Y. Maekawa (LL12–13, 0-10; A1–3, in soil).

Biology. Forest; ground level.

Genus *Prionopelta* Mayr, 1866

Named Bornean species: 1 (Pfeiffer et al. 2011). Lambir species: 1 (named).

Prionopelta kraepelini Forel, 1905 (sp. 1 of SKY)

Collection data. 8 ha plot: w, 18.iv.1993, SKY.

Biology. Forest; ground level.

Genus *Stigmatomma* Roger, 1859

Named Bornean species: 0 (Pfeiffer et al. 2011, genus '*Amblyopone*' recorded). Lambir species: 2 (unidentified). Both species were collected from soil in the forest. Most of the Asian species of this genus had been assigned to the genus *Amblyopone* Roger, 1859, which is confined to Australia, New Guinea etc. (Yoshimura & Fisher 2012).

Unidentified species in *Stigmatomma*: '*Amblyopone*' **sp. 1 of SKY** (8 ha plot, 'Lambir'), '*Amblyopone*' **sp. 13 of SKY** ('Lambir').

Subfamily Ponerinae

Tribe *Platythyreini* Emery, 1901Genus *Platythyrea* Roger, 1863

Named Bornean species: 2 (Pfeiffer et al. 2011). Lambir species: 3 (2 named, 1 unidentified).

Platythyrea parallela (F. Smith, 1859) (sp. 2 of SKY)

Collection data. 8 ha plot: w, 11.i.1993, SKY; fq, 14.i.1993, Tree Tower I, 16 m above ground, at night, SKY; w, wq & m, 10.viii.1995, under bark of fallen tree, SKY (95-L-06).

Biology. Forest; lower vegetation to arboreal; nest under bark of fallen tree.

Platythyrea tricuspidata Emery, 1900 (sp. 1 of SKY)

Collection data. 8 ha plot: fq, 3.iii.1997, SKY.

Unidentified species in *Platythyrea*: **sp. 10 of SKY** (8 ha plot; CA1052).

Tribe *Ponerini* Lepeletier, 1835*Harpegnathos* Jerdon genus groupGenus *Harpegnathos* Jerdon, 1851

Named Bornean species: 2 (Pfeiffer et al. 2011). Lambir species: 1 (named).

Harpegnathos venator (F. Smith, 1858) (sp. 1 of SKY)

Collection data. 8 ha plot: w, 23.i.1993, SKY. ‘Lambir’: w, 18.viii.2003, T. Matsumoto.

Taxonomic notes. We have examined only two worker specimens of this genus from Lambir. In the second specimen the gastral tergites have very weak sculpture and are somewhat shiny, the condition approaching that of the holotype queen of *H. hobbyi* Donisthorpe, 1937 described from Sarawak. However, in other respects the specimen cannot be decisively separable from the first specimen and those from continental Asia. Here we tentatively treat these two specimens as belonging to the widely distributed *H. venator*.

Biology. The first specimen was collected in a forest gap in 8 ha plot.

Hypoponera Santschi genus groupGenus *Hypoponera* Santschi, 1938

Named Bornean species: 3 (Pfeiffer et al. 2011). Lambir species: 15 (all unidentified).

Hypoponera is a large genus with most species living underground. It includes taxonomically difficult species, many of which await to be described. In Lambir most species live in the forest and nest underground.

***Hypoponera cf. mesoponeroides* (Radchenko, 1993) (sp. 21 of SKY)**

Collection data. 8 ha plot: w, 23.1.1993, SKY; w, 30.i.1993, SKY; w, 2.viii.1995, SKY; w, wq & m, 30.vi.2004, rotting wood, SKY (SR04-SKY-51). Tourist area: w, 25.i.1993, SKY.

Taxonomic notes. *Hypoponera mesoponeroides* was originally described from northern Vietnam by Radchenko (1993) as a species of *Brachyponera*. It resembles *Brachyponera* species in having a relatively large body size and the distinctly interrupted dorsal outline of the mesosoma in profile view; the propodeum is lower than pro-mesonotum, and the metanotal groove is distinct. It was recently transferred to *Hypoponera* (Dang et al. 2018). Specimens from Borneo are very similar to those from Vietnam in size, structure and coloration.

Biology. Forest; ground level; nest in rotting wood.

Unidentified species in *Hypoponera*: **sp. 1 of SKY** (8 ha plot, 50 ha plot), **sp. 2 of SKY** (8 ha plot, Tourist area, 50 ha plot, ‘Lambir’; in soil), **sp. 4 of SKY** (8 ha plot, Tourist area, Bt. Pantu), **sp. 5 of SKY** (8 ha plot), **sp. 9 of SKY** (8 ha plot, ‘Lambir’; in soil) **sp. 15 of SKY** (Tourist area, ‘Lambir’; in soil), **sp. 16 of SKY** (Tourist area), **sp. 18 of SKY** (8 ha plot, Tourist area), **sp. 19 of SKY** (8 ha plot), **sp. 21 of SKY** (8 ha plot, Tourist area), **sp. 22 of SKY** (8 ha plot), **sp. 42 of SKY** (8 ha plot), **sp. 46 of SKY** (Tourist area), **sp. 51 of SKY** (‘Lambir’: in soil).

***Odontomachus* genus group**

Recently the former *Pachycondyla* was divided into several genera by Schmidt & Shattuck (2014). Five Bornean genera (*Brachyponera*, *Buniapone*, *Euponera*, *Mesoponera* and *Pseudoneoponera*) in this genus group belong to the former *Pachycondyla*. *Pachycondyla vidua* (F. Smith, 1857) was described from Borneo based on the male and its present status is unknown (Schmidt & Shattuck 2014).

Genus *Anochetus* Mayr, 1861

Named Bornean species: 9 (Pfeiffer et al. 2011). Lambir species 8 (4 named, 4 unidentified).

***Anochetus graeffei* Mayr, 1870 (sp. 3 of SKY)**

Collection data. Tourist area: w, 20.i.1993, SKY.

Taxonomic notes. This wide-ranging species (type locality: Samoa) can be a tramp, but has a notable variation among different localities, suggesting that it is actually a species complex.

Biology. Forest; ground level. The species is rare in Lambir.

***Anochetus myops* Emery, 1893 (sp. 1 of SKY)**

Collection data. 8 ha plot: w, 22.i.1993, SKY; w, 23.i.1993, SKY. Tourist area: w, 11.i.1993, SKY; w, 22.i.1993, SKY. 50 ha plot: 22.viii.1995, SKY.

Biology. Forest; ground level.

Anochetus rugosus (F. Smith, 1857) (sp. 2 of SKY)

Collection data. Tourist area: w, 24.i.1993, SKY. 50 ha plot: w, 24.iii.2013, SKY. 'Lambir': w, 2.i.1998, SKY.

Biology. Forest; ground level.

Anochetus tua Brown, 1978 (sp. 12 of SKY)

Collection data. Tourist area: w, 15.viii.1997, night, SKY. 'Lambir': w, 27.vi.20014, night, SKY.

Biology. Forest; ground level; active in the night.

Unidentified species in *Anochetus*: **sp. 4 of SKY** ('Lambir': forest floor; SQ1184 & GAAP7L9HL07), **sp. 7 of SKY** (8 ha plot), **sp. 9 of SKY** (8 ha plot), **sp. 31 of SKY** ('Lambir'; ex soil).

Genus *Brachyponera* Emery, 1900

Named Bornean species: 4 (Pfeiffer et al. 2011, as species of *Pachycondyla*; Yamane 2007, as species of *Pachycondyla*). Lambir species: 1 (unidentified). The records of *B. luteipes* (Mayr, 1862) and *B. obscurans* (Walker, 1859) from Borneo (Pfeiffer et al. 2011) are doubtful. *Brachyponera pilidorsalis* Yamane, 2007 is common in Sabah, but has not yet been found in Lambir. Yamane & Nona (1994) recorded three species in this genus, but two of them should belong to another genus. In the only Lambir species (sp. 1 of SKY) the mandible lacks a basal fovea.

Unidentified species in *Brachyponera*: **sp. 1 of SKY** (= *Pachycondyla* sp. 28 of SKY; very common in the area surveyed; forest, ground level, active in the daytime, attracted to honey baits; Yamane et al. 1996, as *Brachyponera* aff. *luteipes*; Tanaka et al. 2007).

Genus *Buniapone* Schmidt et Shattuck, 2014

Named Bornean species: 1 (Pfeiffer et al. 2011, as species of *Pachycondyla*). Lambir species: 1 (named).

Buniapone amblyops (Emery, 1887) (sp. 1 of SKY; = *Pachycondyla* sp. 21 of SKY)

Collection data. 'Lambir': wq, 2–4.viii.1995, SKY. 8 ha plot: w & fq, 20.i.1993, SKY.

Biology. Forest; ground level.

Genus *Euponera* Forel, 1891

Named Bornean species: 1 (Pfeiffer et al. 2011, as species of *Pachycondyla*). Lambir species: 1 (named).

Euponera sharpi Forel, 1901 (sp. 1 of SKY; = *Pachycondyla* sp. 1 of SKY)

Collection data. 8 ha plot: w, wq & m, 14.i.1993, SKY. Tourist area: w, 30.xii.1997, SKY. Inoue trail: w, 2.vii.2004, SKY (SR04-SKY-72). 'Lambir': 3w, 12.i.2012, in soil, Y. Maekawa; wq, 18.i.2012, in soil, Y. Maekawa.

Biology. Forest; ground level; nest in soil.

Literature. Yamane & Nona (1994; as *Trachymesopus sharpi*). Ohashi et al. (2017; nest CO₂ emission)

Genus *Leptogenys* Roger, 1861

Named Bornean species: 12 (+5 subspecies). Lambir species: 11 (7 named, 4 unidentified). A salticid spider, *Agorius hyodoi* Yamasaki, 2020, is said to mimic *Leptogenys* species in Lambir (Yamasaki et al. 2020).

Leptogenys chalybaea Emery, 1887 (sp. 4 of SKY)

Biology. Forest; ground level.

Literature. Arimoto & Yamane (2018).

Leptogenys diminuta (F. Smith, 1857) (sp. 3 of SKY) (Pl. 1: 1)

Collection data. 8 ha plot: w, 6.i.1993; w, 11.i.1993, w, SKY; 30.i.1993, SKY; w, 19.iv.1993, SKY; w, 16.xii.1993, w, 11.viii.1995. Bt. Pantu: w, 16.i.1993, SKY; w, 2.i.1998, F. Yamane. 50 ha plot: 7.i.1993, SKY. ‘Lambir’: w, 5.xi.1998, H. Arakawa. *Biology.* Forest; ground level; carnivorous; attracted to honey and cheese baits; active in the daytime. This is the most common *Leptogenys* in Lambir, foraging on ground surface.

Literature. Hashimoto et al. (1997).

Leptogenys cf. hysterica Forel, 1900 (sp. 2 of SKY; =*sp. 5 of SKY*)

Collection data. 8 ha plot: w, 16.i.1993, SKY. ‘Lambir’: w, 3.viii.1995, H. Okido.

Biology. Forest; ground level.

Leptogenys kanaoi Arimoto, 2017 (sp. 12 of SKY)

Biology. Forest; ground level.

Literature. Arimoto (2017).

Leptogenys kitteli transiens Forel, 1911 (sp. 10 of SKY)

Collection data. 50 ha plot: w, 22.viii.1995, SKY.

Biology. Forest; ground level.

Leptogenys myops (Emery, 1887) (sp. 12 of SKY)

Collection data. 8 ha plot: w, 2.viii.1995, from soil, SKY.

Biology. Forest; ground level.

Leptogenys peuqueti (André, 1887) (sp. 11 of SKY)

Collection data. ‘Lambir’: w, 15.viii.1997, SKY; w, 12.viii.1997, Y. Hashimoto.

Biology. Forest; ground level.

Leptogenys processionalis distinguenda (Emery, 1887) (sp. 1 of SKY) (Pl. 1: 2)

Collection data. 8 ha plot: w, 15.i.1993, SKY; w, 22.i.1993, SKY; w, 31.i.1993; w, 3.viii.1995, SKY; w, 21.viii.1995, SKY. Tourist area: w, 22.i.1993, SKY. Bt. Pantu: 13.viii.1995, SKY. 50 ha plot: w, 12.i.1993. HQ: w, 1–3.iii.1997, SKY. ‘Lambir’: 14.vii.1998, H. Arakawa.

Biology. Forest; ground level; attracted to cheese baits; activity high during the night.

In one case many workers were attracted to honey baits, and powdered cheese, which was then covered with soil by them.

Literature. Hashimoto et al. (1997).

Unidentified species in *Leptogenys*: **sp. 6 of SKY** (cf. *L. mutabilis*; common species at ground level), **sp. 16 of SKY** ('Lambir'), **sp. 39 of SKY** (cf. *L. mutabilis*; common species at ground level).

Genus *Mesoponera* Emery, 1900

Named Bornean species: 1 (Pfeiffer et al. 2011, as species of *Pachycondyla*). Lambir species: 3 (unidentified). All the Lambir species are found on the forest floor.

Unidentified species in *Mesoponera*: **sp. 1 of SKY** (= *Pachycondyla* sp. 7 of SKY; 8 ha plot), **sp. 2 of SKY** (= *Pachycondyla* sp. 13 of SKY; 'Lambir', 8 ha plot; nest in soil), **sp. 4 of SKY** (= *Pachycondyla* sp. 9 of SKY; 'Lambir'; nest in soil).

Genus *Myopias* Roger, 1861

Named Bornean species: 7 (Probst et al. 2015; Jaitrong et al. 2020). Lambir species: 2 (1 named, 1 unidentified).

Myopias striaticeps Jaitrong, Wiwatwitaya et Yamane, 2020 (sp. 1 of SKY)

Collection data. Tourist area: w, 20.i.1993, SKY.

Biology. Forest; ground level.

Literature. Jaitrong et al. (2020).

Unidentified species in *Myopias*: **sp. 4 of SKY** (8 ha plot; forest, ground level).

Genus *Odontomachus* Latreille, 1804

Named Bornean species: 5 (Pfeiffer et al. 2011, Satria et al. 2015). Lambir species: 1 (named). The extreme paucity of *Odontomachus* ants characterizes the ant fauna of Lambir. Yamane & Nona (1994) recorded *O. latidens* but this was based on misidentification. To date only a few workers of *O. rixosus* have been collected. Even the 'tramp' species *O. simillimus* F. Smith, 1858, has not yet been encountered.

Odontomachus rixosus F. Smith, 1857 (sp. 2 of SKY)

Collection data. 8 ha plot: w, 16.ii.1995, Abd. Rahman Nona. Bt. Lambir: w, 13–14.viii.1995, Kerangas forest, J. Otsubo.

Biology. So far only three workers have been collected in Lambir, of which two were found in a Kerangas forest.

Literature. Satria et al. (2015).

Genus *Odontoponera* Mayr, 1862

Named Bornean species: 2 (Pfeiffer et al. 2011). Lambir species: 2 (named). *Odontoponera denticulata* had long been treated as a junior synonym of *O. transversa*

until Yamane (2009) showed that both are good species inhabiting different types of habitat.

Odontoponera denticulata (F. Smith, 1858) (sp. 1 of SKY) (Pl. 2: 7, 8)

Collection data. HQ: wq, 19.viii.1995, H. Okido. ‘Lambir’: w, 10.viii.1995, forest edge, SKY; wq, 20.viii.1995, Y. Hashimoto (M95080349).

Biology. Disturbed area; ground level; nest in soil; winged queens attracted to light. This is a common ponerine around the headquarters and forest edges. Nests are dug underground in almost bare land, with many entrance holes and a complicated tunnel system.

Literature. Yamane (2009).

Odontoponera transversa (F. Smith, 1857) (sp. 2 of SKY)

Collection data. 8 ha plot: w, 13.i.1993, SKY (GN-2-1); w, 16.i.1993, SKY; w, 30.i.1993, SKY; w, 30.viii.1993, sugar bait, T. Itino; . Bt. Pantu: w, 16.i.1993, SKY. Tourist area: w, 4.viii.1995, H. Okido; w, 1.i.1998, SKY. ‘Lambir’: w, 14.v.2011, M. Ohashi (LC16, A1–6, in soil; LC18, A1–3, in soil).

Biology. Forest; ground level; nest in soil; attracted to honey and cheese baits; active day and night. This species inhabits good forests, and is never found in highly disturbed areas around Lambir.

Literature. Itino & Yamane (1995), Yamane et al. (1996), Hashimoto et al. (1997; as *O. transversa nitens*), Yamane (2009), Ohashi et al. (2017; nest CO₂ emission).

Genus *Pseudoneoponera* Donisthorpe, 1943

Named Bornean species: 3 (+ 2 subspecies; as forms of *Pachycondyla*). Lambir species: 1 (named).

Pseudoneoponera tridentata (Forel, 1901) (sp. 1 of SKY; =*Pachycondyla* sp. 6 of SKY, part) (Pl. 1: 3, 4)

Collection data. 8 ha plot: w, 1.i.1998, at night, SKY.

Taxonomic notes: This is the largest species among the Bornean *Pseudoneoponera* (Anati et al. in prep.). It is separated from other species by the posteroventrally acute subpetiolar process.

Biology. Forest, ground level, active at the night. Workers release strings of foam from the sting when disturbed (Pl. 1: 4).

Literature. Yamane & Nona (1994; as *Bothroponera tridentata*), Hashimoto & Yamane (2014; prey of army ants).

Plectoctena F. Smith genus group

Genus *Centromyrmex* Mayr, 1866

Named Bornean species: 0 (Pfeiffer et al. 2011 recorded the genus only). Lambir species: 2 (named). One of them, *C. feae*, is rather common in Thailand and Indo-China,

but very rare in Borneo. Both species are new to Borneo.

**Centromyrmex feae* (Emery, 1889) (sp. 2 of SKY)

Collection data. Bt. Lambir: w, 22.viii.1995, Y. Hashimoto (M95080375).

**Centromyrmex hamulatus* (Karavaiev, 1925) (sp. 1 of SKY)

Collection data. 'Lambir': wq, 2–4.viii.1995, SKY.

Biology. The specimen was captured flying close to the forest floor in the daytime.

Ponera Latreille genus group

Recently the former *Pachycondyla* was divided into several genera by Schmidt & Shattuck (2014). Two Bornean genera (*Ectomomyrmex* and *Parvaponera*) in the *Ponera* genus group belong to the former *Pachycondyla*.

Genus *Cryptopone* Emery, 1893

Named Bornean species: 1 (Pfeiffer et al. 2011). Lambir species: 3 (2 named, 1 unidentified). Two named species recorded herein are not found in Pfeiffer et al. (2011). We doubt the occurrence of *C. testacea* (Motschoulsky, 1863) described based on the queen caste from Sri Lanka and recorded by Pfeiffer et al. (2011).

**Cryptopone butteli* Forel, 1913 (sp. 14 of SKY)

Collection data. 8 ha plot: 20.i.1993, SKY. Sungai Liku: w & fq, 27.vi.2004, S SKY. 'Lambir': w, 8.viii.2008, M. Yoshima (80-L2/YM-0816); w, 31.x.2008, M. Yoshima (7-L13/YM-0665).

Taxonomic notes: This is a very distinctive species, having an anteriorly sharply pointed propodeum at the middle of the metanotal groove (seen in dorsal view), and rather thin scale-like petiole (Wheeler 1933). The mandible has five teeth, with the subapical tooth very small.

Biology. Forest; ground level.

Cryptopone sarawakana Wheeler, 1933 (sp. 1 of SKY; =*Hypoconera* sp. 12 of SKY)

Collection data. 8 ha plot: w, 26.i.1993, SKY. Tourist area: w, 30.vi.2004, SKY. 'Lambir': fq, 26.i.1993, Rahman Nona.

Taxonomic notes: This is a distinct species with 6-toothed mandibles, and the head longer than broad.

Biology. Forest; ground level. This is one of the most common species of *Cryptopone* in Borneo. Most samples from Sabah were collected with soil sifting.

Unidentified species in *Cryptopone*: **sp. 3 of SKY** (= *Hypoconera* sp. 10 of SKY; 8 ha plot; forest, ground level).

Genus *Diacamma* Mayr, 1862

Named Bornean species: 4 (+1 subspecies; Pfeiffer et al. 2011). Lambir species: 2 (named). Lambir lacks the most common species in Borneo, '*D. vagans* (F. Smith, 1860)'

(cf. Laciny et al. 2015), which generally occurs in secondary forests and more disturbed areas.

Diacamma intricatum (F. Smith, 1857) (sp. 10 of SKY) (Pl. 1: 5, 6)

Collection data. 8 ha plot: w, 6.i.1993, SKY; w, 13.i.1993, SKY; w, 19.iv.1993, SKY; w, 27.viii.1994, T. Itioka & T. Yumoto. Tourist area: w, 1.i.1998, SKY. Bt. Pantu: w, 16.i.1993, SKY; 23.iii.2013, SKY. Bt. Lambir: 12.i.1993, <400 m alt., SKY. ‘Lambir’: w, 20.viii.1993, sugar bait, T. Itino.

Biology. Forest; ground level; nests in soil; collecting live and dead arthropods (Pl. 1: 5, 6); attracted to *Endospermum* EFN, and honey and cheese baits; active in the daytime.

Literature. Itino & Yamane (1995), Yamane et al. (1996), Hashimoto et al. (1997), Ohashi et al. (2017; nest CO₂ emission).

Diacamma rugosum (Le Guillou, 1842) (sp. 7 of SKY)

Collection data. 8 ha plot: w, 14.i.1993, SKY; w, 27.viii.1994, T. Itioka & T. Yumoto (#70, 73). HQ: 1–3.iii.1997, SKY.

Biology. Forest edge and disturbed area; ground level.

Genus *Ectomomyrmex* Mayr, 1867

Named Bornean species: 4 (Pfeiffer et al. 2011, as species of *Pachycondyla*). Lambir specie: 3 (1 named, 2 unidentified). Among the four species recorded from Borneo by Pfeiffer et al. (2011), *E. apicalis* (F. Smith, 1858) was described based on a dealate queen from Borneo, and its status is unsettled; *E. astutus* (F. Smith, 1858) was originally described from Australia and has been considered a very wide-ranging species, but we doubt if it actually occurs in Borneo. Our *E. cf. javanus* is no doubt a close relative of *E. astutus* and also similar to *E. obtusus* Emery, 1900 described from Borneo.

Ectomomyrmex cf. javanus Mayr, 1867 (sp. 1 of SKY; =*Pachycondyla* sp. 25 of SKY)

Collection data. 8 ha plot: w, 30.xii.1997, SKY; w, 3.i.1998, SKY. Inoue trail: w, 2.vii.2004, in soil, SKY (SR04-SKY-44).

Biology. Forest; ground level; nests in soil.

Literature. Yamane et al. (1996; as *Pachycondyla astutus*)

Ectomomyrmex leeuwenhoekei (Forel, 1886) (sp. 7 of SKY; =*Pachycondyla* sp. 2 of SKY)

Collection data. ‘Lambir’: w, 5.ix.2003, T. Matsumoto (GAAP4L, 7HS09). Tourist area: w, 20.i.1993, SKY. Sungai Liku: w, 23.iii.2013, leaf litter, SKY.

Biology. Forest; ground level.

Unidentified species in *Ectomomyrmex*: **sp. 10 of SKY** (= *Pachycondyla* sp. 39 of SKY; close relative of *E. annamitus* (André, 1892) of the continental Asia; Tourist area),

Genus *Emeryopone* Forel, 1912

Named Bornean species: 1 (Pfeiffer et al. 2011). Lambir species: 1 (named).

Emeryopone buttelreepeni Forel, 1912 (sp. 1 of SKY)

Collection data. ‘Lambir’: w, 26.i.1993, Abd. Rahman Nona; w, 15.vii.2010, M. Ohashi (LL3-42, 10–30, A5 in soil).

Biology. Forest; ground level; nests in soil.

Genus *Parvaponera* Schmidt et Shattuck, 2014

Named Bornean species: 1 (Pfeiffer et al. 2011, as species of *Pachycondyla*). Lambir species: 1 (named).

Parvaponera darwini (Forel, 1893) (sp. 1 of SKY)

Collection data. ‘Lambir’: wq, 14–19.viii.1997, SKY.

Biology. No information is available about its habitat and nesting habits. Queens are attracted to light.

Genus *Ponera* Latreille, 1804

Named Bornean species: 1 (Pfeiffer et al. 2011). Lambir species: 6 (unidentified). The only *Ponera* species recorded from Borneo, *P. borneensis* Taylor, 1967, is a mountain inhabitant and absent from Lambir. Most species inhabit the forest floor, nesting in soil.

Unidentified species of *Ponera* from Lambir: **sp. 1 of SKY** (8 ha plot, Tourist area, 50 ha plot; ‘Lambir’: F-13/SQ1040), **sp. 2 of SKY** (8 ha plot, 50 ha plot), **sp. 4 of SKY** (8 ha plot), **sp. 8 of SKY** (‘Lambir’: 115/SQ1176, F52/SQ-1017), **sp. 9 of SKY** (8 ha plot), **sp. 11 of SKY** (=sp. 24 of SKY; 8 ha plot, 50 ha plot), **sp. 30 of SKY** (‘Lambir’).

Subfamily Dorylinae

Asian Dorylinae include 13 genera, of which nine occur in the Sundaland areas. Two genera distributed in Borneo, *Cerapachys* F. Smith, 1857 and *Yunodorylus* Xu, 2000, have not yet been found in Lambir.

Genus *Aenictus* Shuckard, 1840

Named Bornean species: 26 (Pfeiffer et al. 2011; Jaitrong & Yamane 2011, 2013; Jaitrong & Hashimoto 2012; Jaitrong & Wiwatwitaya 2013; Yamane & Wang 2015). Lambir species: 18 (all named). One species, *A. breviceps*, is recorded from Borneo for the first time. Biology of Lambir species was studied by Yamane & Hashimoto (1999), Matsumoto et al. (2009) and Hashimoto & Yamane (2014). The encounter rate of *Aenictus* colonies was highest in the primary forest than in other forest types (Matsumoto et al. 2009). Sympatric species used different strata from ground surface to canopy and different ant groups/species as their prey (Hashimoto & Yamane 2014).

A. ceylonicus (Mayr)-group

Aenictus jawadwipa Jaitrong et Yamane, 2013 (sp. 24 of SKY)

Collection data. 8 ha plot: w, 26.vi.2004, night, SKY (SR04-SKY-13). Inoue trail: w, 24.iii.2013, night, SKY (SR04-SKY-45).

Biology. Forest; ground level; mainly encountered in the night.

Literature. Jaitrong & Yamane (2013).

A. currax Emery-group

Aenictus cornutus Forel, 1900 (sp. 16 of SKY)

Collection data. ‘Lambir’: w, 26.ix.2006, T. Matsumoto (GAAP5HC23).

Biology. This species is known to forage on both ground level and trees.

Literature. Matsumoto et al. (2009), Jaitrong & Yamane (2011).

Aenictus glabrinotum Jaitrong et Yamane, 2011 (sp. 54 of SKY)

Collection data. 8 ha plot: w, 21.i.1993, Abd. Rahman Nona & SKY.

Biology. This species is known to forage on both ground level and trees.

Literature. Matsumoto et al. (2009), Jaitrong & Yamane (2011).

Aenictus gracilis Emery, 1893 (sp. 19 of SKY)

Collection data. 8 ha plot: w, 18.iv.1993, SKY; w, 16.xii.1993, SKY; w, 11.viii.1995, SKY. Inoue trail: w, 20.viii.1995, SKY; w, 2.vii.2004, daytime, SKY (SR04-SKY-46). Tourist area: 1.i.1998, SKY. Bt. Pantu: w, 16.i.1993, SKY.

Biology. Forest; ground level. Most colonies were collected during the daytime on the forest floor. According to Hirosawa et al. (2000) in Sabah this species mainly forages on trees, hunting *Technomyrmex*, *Paratrechina* (s. lat.) and *Crematogaster*. In Lambir a similar trend for prey selection was confirmed by Hashimoto & Yamane (2014).

Literature. Matsumoto et al. (2009), Jaitrong & Yamane (2011), Hashimoto & Yamane (2014).

Aenictus pfeifferi Zettel et Solger, 2010 (sp. 1 of SKY)

Collection data. 8 ha plot: w, 17.viii.1995, SKY (L-95-20); w, 30.vi.2004, SKY (SR04-SKY-34). Bt. Pantu: w, 13.viii.1995, SKY. ‘Lambir’: 17.viii.1995, forest floor, H. Okido.

Biology. Forest; ground level.

Literature. Jaitrong & Yamane (2011).

A. hottai Terayama et Yamane-group

Aenictus hottai Terayama et Yamane, 1989 (sp. 10 of SKY)

Collection data. Tourist area: w, 24.i.1993, daytime, SKY.

Biology. Primary forest; ground level.

Literature. Matsumoto et al. (2009), Wiwatwitaya & Jaitrong (2011).

A. inflatus Yamane et Hashimoto-group

Aenictus inflatus Yamane et Hashimoto, 1999 (sp. 12 of SKY)

Collection data. 8 ha plot: w, 30.vi.2004, night, SKY (SR04-SKY-35). Tourist area: w, 2.iii.1997, night, SKY (SKYYH-A-6; type series). HQ: 1–3.iii.1997, SKY. ‘Lambir’: w, 25.ix.2003, T. Matsumoto (GAAF3HC65); w, 19.ix.2006, HOT (#HOT-216, WFL); w, 29.ix.2006, HOT (AT1401).

Biology. This peculiar species with an inflated propodeum had been recorded only from Lambir for a long time since it was first discovered in 1997 (Yamane & Hashimoto 1999). Recently it was collected from trees in Jambi, Sumatra (Nazarreta et al. 2019). The large gland in propodeum is full of a red fluid that dissolves in 80 % alcohol very quickly; the function of this fluid is not known but it may be used to pacify prey ants during raiding. This species inhabits both primary forests and secondary forests (Matsumoto et al. 2009), is mainly nocturnal and forages on lower vegetation, occasionally marching on the forest floor. In Lambir main prey of this species were strangely *Paratrechina longicornis* (Latreille, 1802), a famous tramp ant, and *Monomorium* species with a lower frequency (Hashimoto & Yamane 2014).

Literature. Yamane & Hashimoto (1999), Matsumoto et al. (2009), Jaitrong & Yamane (2011), Hashimoto & Yamane (2014).

A. javanus Emery-group***Aenictus javanus*** Emery, 1896 (sp. 21 of SKY)

Collection data. 8 ha plot: w, 11.vii.2004, daytime, HOT (ATO467; erroneously printed as TY04-801 on the data label).

Biology. Forest; ground level.

Literature. Jaitrong & Yamane (2012).

A. laeviceps (F. Smith)-group****Aenictus breviceps*** Forel, 1912 (sp. 29 of SKY)

Collection data. Bt. Pantu: w, 25.iii.2013, daytime, SKY (SR13-SKY-46).

Biology. Forest; ground level. First record for Borneo.

Aenictus fulvus Jaitrong et Yamane, 2011 (sp. 2 of SKY)

Collection data. 8 ha plot: w, 14.i.1993, at night, SKY; w, 17.viii.1995, SKY; w, 26.vi.2004, at night, SKY (SR04-SKY-12).

Biology. Forest; ground level; active day and night.

Literature. Jaitrong & Yamane (2011).

Aenictus laeviceps (F. Smith, 1857) (sp. 18 of SKY, part) (Pl. 2: 9, 10)

Collection data. 8 ha plot: w, 7.i.1993, SKY; w, 2.viii.1995, SKY; w, 7.viii.1995, SKY. 50 ha plot: w, 22.viii.1995, daytime, SKY. Inoue trail: w, 24.iii.2013, night, SKY (SR13-SKY-37). Bt. Pantu: w, 16.i.1993, SKY. Tourist area: 22.i.1993, SKY; w, 15.xii.1993, SKY (Lambir93-sky-A); w, 30.xii.1997, SKY (SR97-SKY-105); w, 1.i.1998, SKY. Bt. Lambir: w, 12.i.1993, daytime, SKY; w, 22.viii.1995, daytime,

SKY. ‘Lambir’: w, 12.viii.1997, Y. Hashimoto (SA9708166); w, 14.viii.1997, SKY; w, 16.viii.1997, SKY (SA970816-03); w, 3.vii.2004, at night, SKY (SR04-SKY-78); w, 12.v.2011, daytime, SKY (SR11-SKY-05); w, 14.v.2011, at night, near pond, SKY (SR11-SKY-21, 22, probably same colony).

Biology. This is a very common species in the forest, and encountered in both the daytime and night time. Foraging columns are often found on the forest floor but mainly attack arboreal ant nests such as *Camponotus*, *Polyrhachis*, *Crematogaster*, *Dolichoderus*. etc. (Hashimoto & Yamane 2014) (Pl. 2: 10). The results more agree with those in Malay Peninsula (Roscziszewski & Maschwitz 1994) than those in Sabah (Hirosawa et al. 2000), where *A. laeviceps* mainly foraged on ground surface. Workers are occasionally attracted to honey baits.

Literature. Hashimoto et al. (1997), Hamaguchi et al. (2007; including *A. sonchaengi* and *A. fulvus*), Matsumoto et al. (2009), Jaitrong & Yamane (2011), Hashimoto & Yamane (2014).

Aenictus sonchaengi Jaitrong et Yamane, 2011 (sp. 8 of SKY)

Collection data. 8 ha plot: w, 22.i.1993, SKY; w, 10.viii.1995, SKY; w, 22.iii.2013, daytime, SKY (SR13-SKY-15). Tourist area: w, 24.i.1993, at night, SKY.

Biology. Forest; ground level; active day and night.

Literature. Jaitrong & Yamane (2011).

A. minutulus Terayama et Yamane-group

Aenictus minutulus Terayama et Yamane, 1989 (sp. 32 of SKY)

Collection data. Canopy 4 ha: w, 12.v.2011, ex soil, SKY (SR11-SKY-12).

Biology. Forest; ground level; trail in soil.

A. pachycerus (F. Smith)-group

Aenictus dentatus Forel, 1911 (sp. 27 of SKY)

Collection data. 8 ha plot: w, 19.iv.1993, SKY; w, 26.vi.2004, at night, SKY (SR04-SKY-11); w, 30.vi.2004, SKY; w, 14.v.2011, daytime, SKY (SR11-SKY-14). Tourist area: w, 2.i.1998, SKY. Bt. Pantu: w, 2.i.1998. ‘Lambir’: w, 28.ii.1997, Y. Hashimoto (SKYYH-A-2); w, 5.xi.1998, H. Arakawa.

Biology. Forest; ground level; active day and night. Most colonies were encountered in primary forests and old secondary forests. Hashimoto & Yamane (2014) listed prey species from five raids; most were *Pheidole* species nesting in soil or on ground surface.

Literature. Matsumoto et al. (2009), Jaitrong et al. (2012), Hashimoto & Yamane (2014).

Aenictus levior (Karavaiev, 1926) (sp. 3 of SKY)

Collection data. Inoue trail: w, 24.iii.2013, daytime, SKY. Tourist area: w, 24.i.1993, at night, SKY. Bt. Pantu: 2.i.1998, daytime, F. Yamane & SKY.

Biology. Forest; ground level; active daytime and night.

Literature. Jaitrong & Yamane (2011).

A. philippinensis Chapman-group

Aenictus punctatus Jaitrong et Yamane, 2012 (sp. 5 of SKY)

Collection data. 8 ha plot: w, 30.vi.2004, at night, SKY (SR04-SKY-38). HQ: 17.viii.1995, H. Okido. 'Lambir': w, 26–30.i.2014, Kitora & Itioka (SQ1009, Q61).

Biology. Forest; ground level (one colony found in the park headquarters).

Literature. Matsumoto et al. (2009), Jaitrong & Yamane (2012).

A. silvestrii Wheeler-group

Aenictus latifemoratus Terayama et Yamane, 1989 (sp. 13 of SKY)

Collection data. Tourist area: w, 20.vi.1998, K. Eguchi (Eg98-BOR-800).

Biology. Forest; ground level.

A. wroughtonii Forel-group

Aenictus camposi Wheeler et Chapman, 1925 (sp. 20 of SKY)

Collection data. 8 ha plot: w, 19.iv.1993, SKY. Tourist area: w, 30.vi.2004, daytime, SKY (SR04-SKY-22).

Biology. This species is mainly diurnal, generally found on the forest floor; no record is available of foraging on trees. In one case in Sabah a trail was found in soil (Yamane, personal observation).

Literature. Matsumoto et al. (2009), Jaitrong & Yamane (2010).

Genus *Dorylus* Fabricius, 1793

Named Bornean species: 2 (Pfeiffer et al. 2011). Lambir species: 2 (named). Pfeiffer et al. (2011) recorded two species, *D. laevigatus* and *D. orientalis* Westwood, 1835 from Borneo. The record for the latter was cited from Chapman & Capco (1951) but Pfeiffer and others were skeptical of its occurrence in Borneo. We also think the record of *D. orientalis* from Borneo was based on misidentification.

Dorylus laevigatus (F. Smith, 1857) (sp. 1 of SKY)

Collection data. 8 ha plot: 5.ii.2005, palm oil trap, HOT (AT1132). HQ: m, 16.xii.1993, at light, SKY. 'Lambir': w, 14.v.2011, near pond, at night, SKY (SR11-SKY-16).

Biology. Forest; ground level; attracted to palm oil traps; males attracted to light.

****Dorylus vishnui*** Wheeler, 1913 (sp. 2 of SKY) (Pl. 2: 11)

Collection data. Tourist area: w, 31.xii.1997, near waterfall, daytime, SKY & F. Yamane (SR97-SKY-111).

Biology. Forest; ground level. The colony we saw was just appearing onto the ground surface in the daytime. New to Borneo.

Genus *Chrysapace* Crawley, 1924

Named Bornean species: 1 (Pfeiffer et al. 2011, as species of *Cerapachys*). Lambir species: 1 (unidentified).

Unidentified species in *Chrysapace*: **sp. 2 of SKY** (= *Cerapachys* sp. 57 of SKY; similar to *jacobsoni* Crawley, 1924, but specifically different; ‘Lambir’: fq, GAAPIL 7HS01).

Genus *Lioponera* Mayr, 1879

Named Bornean species: 3 (Pfeiffer et al. 2011, as species of *Cerapachys*). Lambir species: 6 (3 named, 3 unidentified). All the Lambir species are found in the forest, foraging on the ground surface generally during the daytime.

Lioponera hewitti Wheeler, 1919 (sp. 6 of SKY; = *Cerapachys* sp. 4 of SKY)

Collection data. Bt. Pantu: w, 16.i.1993, SKY. ‘Lambir’: w, 18.viii.1995, Y. Hashimoto (M95080370); w, 21.vi.1998, K. Eguchi (Eg98-BOR-809); w, 23.vi.1998, K. Eguchi (Eg98-BOR-826).

Biology. Forest; ground level.

Lioponera pubescens (Emery, 1902) (sp. 3 of SKY; = *Cerapachys* sp. 3 of SKY)

Collection data. 8 ha plot: w, 7.i.1993, SKY.

Biology. Forest; ground level.

Lioponera suscintata (Viehmeyer, 1913) (sp. 2 of SKY; = *Cerapachys* sp. 26 of SKY)

Collection data. 8 ha plot: w, 3.i.1998, SKY; w, 3.i.1998, F. Yamane. Inoue trail: 24.iii.2013, foraging on ground, SKY (SR13-SKY-29).

Biology. Forest; foraging on ground surface.

Unidentified species in *Lioponera*: **sp. 1 of SKY** (= *Cerapachys* sp. 6 of SKY, close relative of *L. suscintata*; 8 ha plot), **sp. 5 of SKY** (= *Cerapachys* sp. 5 of SKY; close relative of *L. hewitti*; 8 ha plot), sp. 9 of SKY (= *Cerapachys* sp. 15 of SKY; ‘Lambir’: 41-L9/YM-0583), **sp. 15 of SKY** (close relative of *L. hewitti*; ‘Lambir’: TY-10-02).

Genus *Ooceraea* Roger, 1862

Named Bornean species: 0 (Pfeiffer et al. 2011). Lambir species: 3 (unidentified). The Lambir species may belong to the *O. biroi* (Forel, 1907)-complex that can involve several Asian species including undescribed ones. All the Lambir species were collected at the ground level in the forest.

Ooceraea biroi (Forel, 1907)-complex (= *Cerapachys* s.lat. sp. 33 of SKY)

Collection data. ‘Lambir’: w, 15.x.2008 (72-L12/YM-0225); w, 6.v.2011, in soil, M. Ohashi (LL7-47, 0-10, A1).

Biology. Forest; ground level; nest in soil.

Unidentified species in *Ooceraea*: **sp. 2 of SKY** (= *Cerapachys* sp. 2 & 3 of SKY; 8 ha plot: w & fq), and **sp. 5 of SKY** (= *Cerapachys* sp. 7 of SKY; Tourist area: w).

Genus *Parasyscia* Emery, 1882

Named Bornean species: 3 (Pfeiffer et al. 2011, as species of *Cerapachys*). Lambir species: 3 (1 named, 2 unidentified).

Parasyscia dohertyi Emery, 1902 (sp. 14 of SKY; =*Cerapachys* sp. 1 of SKY)

Collection data. 8 ha plot: w, 21.i.1993, SKY; w, 18.viii.1995, SKY; w, 19.viii.1997, SKY. Tourist area: w, 30.vi.2004 (SR04-SKY-32).

Taxonomic notes. Workers are variable in body size. Smaller individuals have a much weaker punctuation on head, mesosoma and gaster than larger ones.

Biology. Forest; ground level.

Unidentified species in *Parasyscia*: **cf. sp. 2 of SKY** ('Lambir'), **sp. 10 of SKY** (= *Cerapachys* sp. 66 of SKY; 8 ha plot: L colony 13-1).

Genus *Syscia* Roger, 1861

Named Bornean species: 0 (Pfeiffer et al. 2011). Lambir species: 3 (unidentified). According to Boroviec (2016) this genus is known to occur on Borneo. All Lambir species are collected at ground level in the forest.

Unidentified species in *Syscia*: **sp. 3 of SKY** (= *Cerapachys* sp. 27 of SKY; Tourist area, 'Lambir'), **sp. 9 of SKY** (= *Cerapachys* sp. 30 of SKY; 'Lambir': CI94), **sp. 10 of SKY** (= *Cerapachys* sp. 8 of SKY; Tourist area).

Subfamily Dolichoderinae

Genus *Chronoxenus* Santschi, 1919

Named Bornean species: 0 (Pfeiffer et al. 2011). Lambir species: 1 (unidentified).

Chronoxenus* cf. *wroughtonii javanus (Forel, 1909) (sp. 1 of SKY)

Collection data. HQ: w, wq & m, 7.viii.1995, SKY (95-L-05).

Biology. Disturbed area; ground level.

Genus *Dolichoderus* Lund, 1831

Named Bornean species: 15 (Pfeiffer et al. 2011). Lambir species: 10 (8 named, 2 unidentified). The *Dolichoderus* fauna of Lambir is rather poor compared with that of Sabah (for example Poring and Danum Valley).

D. cuspidatus (F. Smith)-group (=subgenus *Diabolus* Karavaiev, 1926)

Dolichoderus coniger (Mayr, 1870) (sp. 1 of SKY)

Collection data. 8 ha plot: w, 27.viii.1994, T. Itioka & T. Yumoto (#71); same data, T. Itioka (#127).

Biology. Forest; arboreal.

Literature. Yamane & Nona (1994), Dill (2002).

Dolichoderus cuspidatus (F. Smith, 1857) (sp. 2 of SKY) (Pl. 3: 12, 13)

Collection data. 8 ha plot: w, 13.i.1993, walkway, SKY; w, 15.i.1993, near Tower 1, SKY; w, 27.viii.1994, T. Itioka & T. Yumoto (#87, 91, 94); w, 5.viii.1995, with mealy bags, SKY; w, 18.viii.1995, SKY; w, 20.viii.1995, prey of a predatory bug, SKY; w, 23–24.viii.1995, Tower 2–walkway, SKY; w, 30.xii.1997, walkway; w, 30.xii.1997, SKY; w, 30.xii.1997, walkway, F. Yamane. Tourist area: w, 24.i.1993, SKY; w, 30.i.1993, SKY. Bt. Lambir: w, 22.viii.1995, SKY. ‘Lambir’: w, 10.x.2005, C. Handa (17-4, 17-5).

Biology. Forest; arboreal; nest in tree hollows; attracted to honey and cheese baits; active day and night. This is the most common species of *Dolichoderus* in Lambir. It nests in hollows of big trees (Pl. 3: 12), and takes care of mealy bugs in the nest and foraging site. Foragers climb trees up to the canopy and release mealy bugs on young leaves especially in the night. The symbiosis between *D. cuspidatus* and mealy bugs is reviewed by Dill & Maschwitz (2002). Returning workers very rarely carry solid food in their mandibles. Workers are little interested in insects even if the latter are placed in front of them (Pl. 2: 13). Predatory bugs hunt worker ants of this species around their nests.

Literature. Hashimoto et al. (1997), Dill (2002), Dill & Maschwitz (2002), Tanaka et al. (2012), Hashimoto & Yamane (2014; prey of army ants), Katayama et al. (2015; supporting information).

D. scabridus Roger-group (=subgenus *Diceratoclinea* Wheeler, 1935)

Dolichoderus beccarii Emery, 1887 (sp. 4 of SKY)

Collection data. 8 ha plot: w, 20.i.1993, SKY; w, 26.i.1993, SKY; w, 9.viii.1994, T. Itioka (8/9-14); w & m, 3.viii.1995, nesting among dead leaves on tree, SKY; w, 10.viii.1995. Canopy 4 ha: w, 2.vii.2004, SKY (SR04-SKY-81). Sungai Liku: w, 23.iii.2013, EFN of *Shorea* seedlings, SKY.

Biology. Forest; lower vegetation to arboreal; attracted to extrafloral nectary. A nest was found from a mass of dead leaves on a tree.

Literature. Tanaka et al. (2007).

Dolichoderus indrapurensis nigrogaster Viehmeyer, 1922 (sp. 34 of SKY)

Collection data. 8 ha plot: 3.i.1998, SKY; w, 23.ix.2003, HOT (BTA1712, BTA2370); w, v–vi.2003, HOT & T. Itioka (AT0187); w, iii–vi.2003, HOT & T. Itioka (AT0112); w, xii.2003–iii.2004, HOT & T. Itioka (DAT 160).

Taxonomic notes. *Dolichoderus beccarii* was described from a single queen, while *D. indrapurensis* Forel, 1912 was described from the worker caste, both from Sumatra. Most authors suspect that *D. indrapurensis* represents the worker of *D. beccarii*, although queen-worker combination has not yet been established based on colony series (e.g., Forel 1912, Dill 2002). The subspecies *D. i. nigrogaster* was

described based on the worker caste from Brunei, Borneo as a variety of *indrapurensis*. Our specimens from Lambir partly agree with the original description of *D. i. nigrogaster* in the following aspects: head and mesosoma almost black instead of brown in *D. beccarii*, gaster often dark brown, standing hairs on antennal scape and mid-femur and tibia shorter than in the latter. However, the assignment of them to *D. i. nigrogaster* remains tentative and we need complete colony series with workers and queens to resolve problems surrounding this species group.

Biology. Forest; arboreal; attracted to honeydew excreted by homopterans on lianas; active in the daytime.

D. sulcaticeps (Mayr)-group

Dolichoderus semirugosus (Mayr, 1870) (sp. 19 of SKY)

Collection data. Tourist area: w, 23.viii.1993, SKY; w, 23.viii.1995, Y. Hashimoto (M950804669); w, same date, SKY.

Biology. Forest; lower vegetation.

Dolichoderus cf. siggi Forel, 1895 (sp. 46 of SKY)

Collection data. ‘Lambir’: w, 3–12.ix.2009 (ant-mimic sample-99.1).

Literature. Hashimoto & Yamane (2014; prey of army ants).

Unidentified species in *D. sulcaticeps* group: **sp. 38 of SKY** (P078-12, AT1050; CR00069), **sp. 50 of SKY** (8 ha plot: 40 m above ground, AT1036).

D. thoracicus (F. Smith)-group

Dolichoderus affinis Emery, 1889 (sp. 10 of SKY)

Collection data. 8 ha plot: 7.ii.2010, HOT (CA1120, CA1106). ‘Lambir’: w, 21–27.ii.2009 (ant-mimic sample-00226.07).

Biology. Forest; arboreal. To date only a few workers have been collected from Lambir for this species, which is common in Sumatra and Indo-Chinese Peninsula.

Literature. Tanaka et al. (2012).

Dolichoderus thoracicus (F. Smith, 1860) (sp. 3 of SKY) (Pl. 3: 14, Pl. 4: 15, 16)

Collection data. 8 ha plot: w, 9.viii.1994, T. Itioka (#135); w, 19.viii.1994, T. Itioka (#129). Tourist area: 25.i.1993, SKY. 50 ha plot: 27.i.1993, SKY. ‘Lambir’: w, 29.vii.1993, T. Itino.

Biology. Forest; arboreal; nest in space made of leaves woven with silk; attracted to honeydew excreted by homopterans, cheese baits; active day and night.

Literature. Tanaka et al. (2007, 2012), Hashimoto & Yamane (2014; prey of army ants), Katayama et al. (2015; supporting information).

Unidentified species in *D. thoracicus* group: **sp. 32 of SKY** (=sp. 47 of SKY; ‘Lambir’: CN181).

Genus *Iridomyrmex* Mayr, 1862

Iridomyrmex anceps (Roger, 1863) (sp. 1 of SKY)

Collection data. 8 ha plot: w, 18.iv.1993, SKY. HQ: wq & m, viii.1995, at light, SKY; w, 3–20.viii.1995, SKY; wq, 10–20.viii.1995, at light, SKY.

Biology. Disturbed area and forest edge; ground level; new queens and males attracted to light.

Genus *Philidris* Shattuck, 1992

Named Bornean species: 2 (Pfeiffer et al. 2011). Lambir species: 2 (1 named, 1 unidentified).

Philidris cordata protensa (Forel, 1911) (sp. 1 of SKY)

Collection data. 8 ha plot: w, 17.viii.1997, SKY. Canopy 4 ha: w, 4.iii.2004, HOT (P3B9); w, wq & m, 4.iii.2004, HOT (P3B10); w & wq, 4.iii.2004, HOT (P3B11). Secondary forest nearby the national park: w, 26.vi.2004, on rattan, SKY (SR04-SKY-03). ‘Lambir’: w, 17.viii.1997, SKY.

Biology. Forest and forest edge; generally arboreal but foragers are also seen on the ground surface; nest in dead branches/twigs; attracted to honey and cheese baits.

Literature. Hashimoto et al. (1997).

Unidentified species in *Philidris*: **cf. sp. 3 of SKY** (8 ha plot: on tree tower).

Genus *Tapinoma* Foerster, 1850

Named Bornean species: 3 (Pfeiffer et al. 2011). Lambir species: 8 (2 named, 6 unidentified). *Tapinoma krakatauae* is recorded from Borneo for the first time.

Tapinoma cf. indicum Forel, 1895 (sp. 1 of SKY)

Collection data. 8 ha plot: w, 30.i.1993, SKY. HQ: w, 30.i.1993, SKY. 7.i.1993, SKY. Secondary forest nearby the national park: w, 12.ix.2003, HOT (BTA1755).

Biology. Forest edge and disturbed area; lower vegetation; attracted to extrafloral nectary including *Endospermum* EFN and honey baits.

Literature. Yamane et al. (1996), Tanaka et al. (2007).

****Tapinoma krakatauae*** (Wheeler, 1924) (sp. 7 of SKY)

Collection data. 8 ha plot: w, xii.2003–iii.2004, HOT & T. Itioka (DAT266); w, 16.ix.2006, HOT (AT1255). ‘Lambir’: w, v–vi.2003, HOT & T. Itioka (AT0210); w, 28–29.vii.2014, Kitora & Itioka (A-1-2, C80, SQ-0989).

Biology. Forest; arboreal. This species was originally described from the Krakatau Islands, Indonesia (see Yamane 2013), and is here recorded from Borneo for the first time. We have specimens also from Sumatra (Yamane unpubl.).

Literature. Tanaka et al. (2012), Katayama et al. (2015; supporting information).

Tapinoma melanocephalum (Fabricius, 1793) (sp. 4 of SKY).

Collection data. 8 ha plot: w, 27.viii.1994, T. Itioka & T. Yumoto (#65).

Literature. Katayama et al. (2015; supporting information).

Unidentified species in *Tapinoma*: **sp. 3 of SKY**, **sp. 5 of SKY** (8 ha plot; arboreal, nest in compartmentalized space under bark, active in the daytime; AT0151, 1217; DAT290; Tanaka et al. 2012), **sp. 9 of SKY** (*'Zatapinoma'*; 8 ha plot; arboreal, nest in dead twig/liana stem, active in the daytime; AT0050, 0090, 0141, 1312; DAT181, 640; Tanaka et al. 2012; Katayama et al. 2015, supporting information), **sp. 10 of SKY** (DAT432; Katayama et al. 2015, supporting information), **sp. 16 of SKY** (*'Zatapinoma'*; Canopy 4 ha; arboreal, nest in dead twigs; P1B5-1, P1B7, P3B6-2, P3B8-2, P6B12, P9B10-1).

Genus *Technomyrmex* Mayr, 1872

Named Bornean species: 27 (Bolton 2007, Pfeiffer et al. 2011). Lambir species: 17 (14 named, 3 unidentified). A single worker of *Technomyrmex brunneus* Forel, 1895 was collected from Brunei, but this probably represents an introduction or perhaps a mislabeling of the specimen (Bolton 2007). The record of *Technomyrmex horni* Forel, 1912 from Borneo by Pfeiffer et al. (2011) may be based on misidentification; the specimens examined by us all seem to be *T. schimmeri* (see below). We recognize 25 named species plus four unidentified species in Borneo.

T. albipes (F. Smith)-group

In Asia this group comprises more than 20 species that are very similar to each other in size, coloration and structure (Bolton 2007). All are small and black ants, generally encountered on forest floor and in lower vegetation, often together with hemipterans, from which ants take honeydew secreted by them (Pl. 4: 17). Many are forest inhabitants, but others are famous tramps.

Technomyrmex albipes (F. Smith, 1861) (sp. 25 of SKY)

Collection data. Inoue trail: w, 2.vii.2004, rotting wood, SKY (SR04-SKY-47).

Biology. Forest; ground level to arboreal; nest in rotting wood; active in the daytime. This is considered a tramp, but is often found in the forest, suggesting the presence of an ecological race or cryptic species.

Literature. Tanaka et al. (2012).

Technomyrmex butteli Forel, 1913 (sp. 2 of SKY)

Collection data. Inoue trail: 8 ha plot: w, 13.i.1993, honey bait, SKY; w, 31.i.1993, honey bait, SKY; w, 27.viii.1994, T. Itioka & T. Yumoto (#100). Tourist area: w, 20.i.1993, SKY. 50 ha plot: w, 27.i.1993, SKY.

Biology. Forest; ground level and lower vegetation; nest in compartmentalized space under bark; attracted to honeydew excreted by homopterans, extrafloral nectary, and honey baits; active day and night.

Literature. Yamane et al. (1996), Tanaka et al. (2007), Hashimoto & Yamane (2014; prey of army ants).

Technomyrmex difficilis Forel, 1892 (sp. 14 of SKY)

Collection data. HQ: 2–20.viii.1995, SKY. 8 ha plot: w, v–vi.2003, HOT & T. Itioka (AT0105, AT0153).

Biology. Forest and disturbed area; ground level to arboreal; active day and night. This is a famous tramp (Bolton 2007).

***Technomyrmex elatior* Forel, 1902 (sp. 27 of SKY)**

Collection data. Inoue trail: 8 ha plot: w, 30.ix.2006, HOT (AT1428). Inoue trail: w, 24.iii.2013, SKY; w, 24.iii.2013, foragers on ground, SKY (SR13-SKY-30); w, 25.iii.2013, foragers on tree, SKY (SR13-SKY-48). Bt. Lambir: w, 21.viii.1995, M. Kato. ‘Lambir’: w, 28.ix.2006, HOT (AT1393); w, 21.x.2013, Kitora & Itioka (CI090).

Biology. Forest; ground level to arboreal; active day and night.

Literature. Katayama et al. (2015; supporting information).

***Technomyrmex modiglianii* Emery, 1900 (sp. 1 of SKY)**

Collection data. 8 ha plot: w, 26.viii.1994, T. Itioka & T. Yumoto; w, 27.viii.1994, T. Itioka & T. Yumoto (#107); w, 17.viii.1995, ex epiphyte #7, SKY; w, 18.ix.2006, walkway, HOT (AT1232); w, 30.ix.2006, HOT (AT1428). Tourist area: w, 25.i.1993, SKY. Bt. Pantu: w, 12.i.1993, SKY; w, 16.i.1993, SKY; w, 2.i.1998, F. Yamane.

Biology. Forest; ground level to arboreal; nest in compartmentalized space under bark and in aerial soil accumulated at bases of epiphytes; active day and night.

Literature. Yamane et al. (1996), Tanaka et al. (2012); Hashimoto & Yamane (2014; prey of army ants); Katayama et al. (2015; supporting information).

***Technomyrmex cf. pluto* Bolton, 2007**

Collection data. 8 ha plot: w, 29.ix.2006, HOT (AT1424).

Taxonomic notes. The worker specimen examined is very similar to the Sulawesi species *T. pluto* in coloration; the caxae, tibiae and tarsi of the mid- and hind legs are whitish yellow, but the petiole is entirely dark brown unlike that of *T. pluto*. In pilosity it is similar to *T. albipes* as mentioned for *T. pluto* by Bolton (2007).

Biology. Forest; ground level to arboreal; nest in compartmentalized space under bark.

***Technomyrmex rotundiceps* Karavaiev, 1926 (sp. 26 of SKY)**

Collection data. 8 ha plot: w, 10.ix.2006, walkway, HOT (AT1187). ‘Lambir’: 28.ix.2006, HOT (AT1373).

Biology. Forest; arboreal. In Sabah this species was also collected on lower vegetation.

Literature. Katayama et al. (2015; supporting information).

***T. bicolor* Emery-group**

***Technomyrmex kraepelini* Forel, 1905 (sp. 4 of SKY)**

Collection data. 50 ha plot: w, 24.iii.2013, SKY. ‘Lambir’: w, 2.i.1998, SKY.

Biology. Forest; lower vegetation.

Technomyrmex lisae Forel, 1913 (sp. 5 of SKY)

Collection data. 8 ha plot: w, 30.vi.2004, cheese bait, SKY (SR04-SKY-66); w, 18.ix.2006, walkway, HOT (AT1245). Tourist area: 22.iii.2013, nest in dead leaves on palm, SKY (SR13-SKY-04). 50 ha plot: w, 27.i.1993, SKY. ‘Lambir’: w, 21.viii.1993, T. Itino; w, 23.viii.1993, T. Itino; w, 23.viii.1995, M. Kato.

Biology. Forest; ground level to arboreal; attracted to sugar and cheese baits; activity high during the night. In Sabah workers were often found under the bark of living trees, but nests were not confirmed.

Literature. Yamane et al. (1996).

Technomyrmex schimmeri Viehmeyer, 1916 (sp. 22 of SKY)

Collection data. Inoue trail: w, 24.iii.2013, SKY. Bt. Lambir: w, 13–14.viii.1995, Kerangas forest, J. Otsubo. ‘Lambir’: w, 31.x.2008, M. Yoshima (7-L17, YM-0690).

Taxonomic notes. This species is very similar to *T. horni* Forel, 1912 described from Taiwan (Bolton 2007). However, they are different in some structural characters (for a redescription of *T. horni*, see Yamane et al. 2018b), suggesting that they are good species. We need DNA information to resolve this problem.

T. grandis Emery-group***Technomyrmex grandis*** Emery, 1887 (sp. 7 of SKY)

Collection data. ‘Lambir’: w, 22.iv.2005, army ant prey (BOTY732A); w & fq, 12.v.2011, nest between two leaves, SKY (SR11-SKY-06).

Biology. Forest; arboreal; nest among woven leaves.

T. pratensis (F. Smith)-group***Technomyrmex pratensis*** (F. Smith, 1860) (sp. 3 of SKY)

Collection data. 8 ha plot: w, 12.i.1993, honey bait, at night, SKY; w, 3.i.1998, SKY; w, 3.iii.1998, F. Yamane. 50 ha plot: w, 24.iii.2013, SKY.

Biology. Forest; ground level and lower vegetation; attracted to honey baits; active in the night.

T. strenuus Mayr-group***Technomyrmex mandibularis*** Bolton, 2007 (sp. 20 of SKY; = *sp. 34 of SKY*)

Collection data. Canopy 4 ha: w, wq & m, 29.ix.2006, 25 m from ground, HOT (AT1408).

Biology. Forest; arboreal.

Technomyrmex strenuus Bolton, 2007 (sp. 32 of SKY)

Collection data. 8 ha plot: fq, 30.xii.1997, walkway, SKY.

Biology. Forest; arboreal. This species constructs carton nests on tree leaves in Sabah and Sumatra.

T. textor Forel-group

Technomyrmex dubius Bolton, 2007 (sp. 17 of SKY)

Collection data. 8 ha plot: w, 2.x.2006, tree tower, HOT (AT1503). ‘Lambir’: w, 15.viii.1997, SKY.

Biology. Forest; arboreal; active at night.

Unidentified species in *Technomyrmex*: **sp. 37 of SKY** (Canopy 4 ha: arboreal, nest in dead twig; P5B11), **sp. 39 of SKY** (‘Lambir’: ant-mimic sample).

Subfamily Ectatomminae

Genus *Gnamptogenys* Roger, 1863

Named Bornean species: 22 (Lattke 2004, Pfeiffer et al. 2011). Lambir species: 11 (5 named, 6 unidentified).

Gnamptogenys binghamii (Forel, 1900) (sp. 23 of SKY)

Collection data. 8 ha plot: w, 31.i.1993, SKY. Inoue trail: w, 2.vii.2004, SKY. Tourist area: w, 21.iii.1993, SKY; w, 30.xii.1997, SKY. ‘Lambir’: w, 22.x.2008, M. Yoshima (A-L/YM-1005).

Biology. Forest; ground level.

Gnamptogenys costata (Emery, 1889) (sp. 2 of SKY)

Collection data. 8 ha plot: w, 11.i.1993, SKY; w, 16.i.1993, SKY; w, 14.viii.1995, SKY; w, 3.iii.1997, SKY. Tourist area: w, 22.i.1993, SKY. ‘Lambir’: w, 14.viii.1995; w, 15.v.2011, SKY.

Biology. Forest; ground level.

Gnamptogenys cribrata (Emery, 1900) (sp. 22 of SKY)

Collection data. 8 ha plot: w, 3.viii.1995, SKY. Tourist area: w, 2.iii.1997, SKY; w, 30.vi.2004, SKY 50 ha plot: w, 27.i.1993, SKY. ‘Lambir’: w, 14.viii.1997, SKY; w, 23.vi.1998, K. Eguchi (Eg98-BOR-827).

Taxonomic notes. The Sundaland samples of this species have been treated as *G. dammermani* (Wheeler 1924) described from Pulau Sebesi in the Sunda straits. *Gnamptogenys cribrata* sensu Lattke (2004) seems a highly variable species, geographically ranging from New Guinea, Philippines, Sundaland to Thailand.

Biology. Forest; ground level; sampled from soil.

Gnamptogenys cf. fontana Lattke, 2004 (sp. 10 of SKY)

Collection data. HQ: w, 25.viii.1995, SKY.

Biology. Disturbed area; ground level.

Gnamptogenys menadensis (Mayr, 1887) (sp. 1 of SKY)

Collection data. 8 ha plot: w, 6.i.1993, SKY; w, 26.i.1993, SKY; w, 9.viii.1994, T. Itioka; w, 27.viii.1994, T. Itioka; w, 1.iii.1997, SKY; w, 30.xii.1997, SKY; w,

30.xii.1997, F. Yamane. 50 ha plot: w, 7.i.1993, SKY. Bt. Lambir: w, 12.i.1993, 400 m alt., SKY. 'Lambir': w, 2.i.1998, SKY; w, 7.vii.1998, H. Arakawa; w, 19.v.2011, S. Hasin.

Biology. Forest; lower vegetation; feeding on insects; attracted to honey and cheese baits; foragers found together with *Polyrhachis* (*Myrmhopla*) *rufipes* on plant leaves.

Literature. Hashimoto et al. (1997).

Gnamptogenys posteropsis (Gregg, 1951) (sp. 12 of SKY)

Collection data. 8 ha plot: w, 11.viii.1995, SKY.

Unidentified species in *Gnamptogenys*: **sp. 4 of SKY** (8 ha plot), **sp. 16 of SKY** (8 ha plot, 50 ha plot), **sp. 18 of SKY** (ex soil), **sp. cf. 39 of SKY** ('Lambir': ex soil), **sp. 45 of SKY** (ex soil).

Subfamily Formicinae

Tribe Camponotini Forel, 1878

Currently eight genera are included in this tribe, of which five have been recorded from Borneo: *Camponotus*, *Colobopsis*, *Dinomyrmex*, *Echinopla* and *Polyrhachis*. All these five are seen in Lambir and constitute important part of ant community.

Genus *Camponotus* Mayr, 1861

Named Bornean species: 52 (DumPERT 1996, Pfeiffer et al. 2011, Zettel et al. 2018). Lambir species: 50 (15 named, 35 unidentified). Pfeiffer et al. (2011) listed 60 species (total 73 forms) of '*Camponotus*' from Borneo, of which one (*gigas*) was transferred to *Dinomyrmex* and 12 to *Colobopsis* (see Ward et al. 2016). Among the true *Camponotus* forms (54) listed by Pfeiffer et al. (2011) some were described based on the queen alone, others are apparently erroneously recorded (*C. barbatus*, *C. compressus* etc.), and many belong to the subgenus *Tanaemyrmex* that is taxonomically the most difficult group full of unresolved problems. This makes it difficult to estimate the real number of species so far known from Borneo. Furthermore, there should be many more undescribed species, especially in the poorly studied subgenus *Myrmamblys*, many of which lead a cryptic life or are involved in mimicry complexes (e.g., Zettel et al. 2018).

Subgenus *Karavaivia* Emery, 1925

Camponotus dolichoderoides Forel, 1911 (sp. 94 of SKY)

Collection data. 8 ha plot: w, 10.viii.1995, night; w, v–vi.2003, HOT & T. Itioka (AT0137). Inoue trail: w, 30.vi.2004, carton nest on tree leaf, SKY (SR04-SKY-33). 'Lambir': w, 27.xii.2001, C. Yoneyama (AHP01-00568); w, v–vi.2003, HOT & T. Itioka (AT0137).

Biology. Forest; ground level to arboreal; carton nest on tree leaves; active at night.

Literature. Tanaka et al. (2010), Katayama et al. (2015; supporting information).

Unidentified species in the subgenus *Karavaievia*: **sp. 146 of SKY** ('Lambir').

Subgenus *Myrmamblys* Forel, 1912

This is a large and very diverse group mainly distributed in the Old World, and is taxonomically very poorly studied. Species discrimination is very difficult in many cases. Not a few species are involved in model-mimic systems (Zettel et al. 2018). Nests are generally found from dead twigs (on the ground surface or trees) or decayed parts of trees.

Camponotus bedoti Emery, 1893 (sp. 31 of SKY)

Collection data. HQ: w, 1–3.iii.1997, SKY. 'Lambir': w, 10.viii.1995, forest edge, SKY.

Biology. Forest and disturbed area; ground level to lower vegetation; attracted to extrafloral nectary.

Literature. Tanaka et al. (2007; as *C. reticulatus*), Katayama et al. (2015; supporting information; as *C. reticulatus*).

Camponotus cf. kutteri Forel, 1915

Collection data. w, xii.2003–iii.2004, HOT & T. Itioka (#DAT10).

Camponotus cf. leucodiscus Wheeler, 1919 (sp. 100 of SKY)

Collection data. 8 ha plot: w, 14.viii.1995, ex epiphyte, T. Yumoto.

Camponotus paracolobopsis Zettel et Yamane, 2018 (sp. 65 of SKY)

Collection data. 8 ha plot: w, 30.xii.1997, walkway, SKY. Canopy 4 ha: w, wq & m, 7.iii.2004, HOT (P7B12-3); w, wq & m, 7.iii.2014 HOT (P7B14); w, 8.iii.2004, HOT (P10B5). 'Lambir': w, 3–12.ix.2009 (ant-mimic sample, #66, 380).

Biology. Forest; arboreal; nests in dead branches/twigs.

Literature. Zettel et al. (2018).

Unidentified species in the subgenus *Myrmamblys*: **sp. 22 of SKY** ('Lambir'; Itino & Yamane 1995, subcanopy, attracted to sugar baits), **sp. 24 of SKY** (8 ha plot; arboreal: AT1399), **sp. 27 of SKY** (8 ha plot; lower vegetation, attracted to EFN; AT0091, BOTY257A05), **sp. 29 of SKY** (50 ha plot; 'Lambir': ant-mimic sample-210; Tanaka et al. 2007), **sp. 35 of SKY** (HQ), **sp. 36 of SKY** (AT1212), **sp. 38 of SKY** (8 ha plot; Canopy 4 ha; arboreal, nest in dead twigs; P2 B11, P6 B4-1, P6 B9-2, P7 B8, P10 B7, P10 B9, dead twigs at 25.4 m above ground), **sp. 43 of SKY** (8 ha plot, 'Lambir'), **sp. 45 of SKY** (8 ha plot; Inoue trail, in dead standing tree, SR04-SKY-40), **cf. sp. 56 of SKY** (8 ha plot), **sp. 68 of SKY** (HQ; 50 ha plot; ant-mimic sample-080725.e9), **sp. 70 of SKY** (8 ha plot), **sp. 101 of SKY** (8 ha plot: AT0691, AT1118), **sp. 102 of SKY** ('Lambir'; lower vegetation, mimicking *Crematogaster inflata*), **sp. 122 of SKY** (8 ha plot; arboreal; AT1399), **sp. 126 of SKY** (8 ha plot; arboreal, active in the daytime, nest

in aerial soil accumulated at base of epiphyte, attracted to EFN; #DAT, 018, 475; Tanaka et al. 2010, 2012), **sp. 134 of SKY** (8 ha plot; arboreal, nest in live liana stem; AT0865, HYT020, AT0343, HYT021), **sp. 144 of SKY** (=sp. 162 of SKY; 8 ha plot, Canopy 4 ha; arboreal, nest in dead twig: P2 B8), **sp. 158 of SKY** ('Lambir'), **sp. 165 of SKY** (Canopy 4 ha; arboreal, nest in dead twig: P4B11), **sp. 171 of SKY** (ant-mimic sample-20121207H50C), **sp. 172 of SKY** ('Lambir': CA1135).

Subgenus *Myrmoplatys* Forel, 1916

All the species of this subgenus live in spiny climber plants of the genus *Korthalsia* (rattans) in the forest (Pl. 4: 18).

Camponotus contractus Mayr, 1872 (sp. 17 of SKY)

Collection data. 50 ha plot: w, 23.viii.1993, ex *Korthalsia echinometra*, T. Itino.

Camponotus hospes (Emery, 1884) (sp. 16 of SKY)

Collection data. 50 ha plot: w & fq, 13.viii.1993, ex *K. rostrata*, T. Itino. 'Lambir': w, 7.viii.1993, T. Itino.

Camponotus korthalsiae Emery, 1887 (sp. 18 of SKY)

Collection data. 50 ha plot: w & wq, 23.viii.1993, ex *K. echinometra*, T. Itino.

Camponotus megalonyx Wheeler, 1919 (sp. 20 of SKY)

Collection data. 8 ha plot: w, 20.viii.1994, T. Itioka (#128). 50 ha plot: w, 23.viii.1993, ex *K. hispida*, T. Itino; w, 26.viii.1993, ex *K. hispida*, T. Itino; w, xii.2003–iii.2004, HOT (GEN029). 'Lambir': w & m, 29.vii.1993, ex *Korthalsia*, T. Itino; w, 13.viii.1993, ex *K. hispida*, T. Itino; w, 27.ix.2003, HOT (LUB03-14706); w, xii.2003–iii.2004, HOT (029).

Unidentified species in the subgenus *Myrmoplatys*: **sp. 19 of SKY** (Tourist area; 50 ha plot: ex *K. formicaria*; Bt. Lambir), **sp. 21 of SKY** (8 ha plot: SR11-SKY-10; Tourist area; Pl. 4: 18).

Subgenus *Myrmosaulus* Wheeler, 1921

Probably *Camponotus singularis rufomaculatus* does not belong to the true *Myrmosaulus* but should be assigned to a separate subgenus (see Bolton 2003).

Camponotus singularis rufomaculatus Donisthorpe, 1941 (sp. 6 of SKY, part)

Collection data. 8 ha plot: w, 21.i.1993, SKY.

Taxonomic notes. Laciny et al. (2016) believe that this form is a distinct species endemic to Borneo. It is characterized by the stout blackish standing hairs on the head and shorter, sparser hairs on the mesosoma. A related species, *C. camelinus* (F. Smith, 1857), occurs in Sabah; it has an entirely black body, while *C. singularis rufomaculatus* has a reddish head.

Biology. Forest; lower vegetation.

Subgenus *Myrmotarsus* Forel, 1912

Relatively large ants inhabiting forests and nest mainly hollow trees. Most species are known to share foraging trails and sometimes nests with species of the *Crematogaster modiglianii* ('*Paracrema*'), and *inflata*-group ('*Physocrema*') (Pl. 5: 21).

Camponotus gilviceps Roger, 1863 (sp. 23 of SKY; =*sp. 11* of SKY)

Collection data. 8 ha plot: w, 26.vi.2004, night, SKY. Tourist area: w, 25.i.1993, SKY; w, 22.viii.1995, SKY; w, 2.iii.1997, SKY. 50 ha plot: w, 7.i.1993, SKY. Bt. Lambir: w, 22.viii.1995, SKY. 'Lambir': w, 30.viii.1993, forest floor, sugar bait, T. Itino.

Biology. Forest; ground level to arboreal; nest in big tree hollow and in aerial soil accumulated at branch forks; attracted to honeydew secreted by homopterans, and sugar baits; active day and night. This species shares foraging trails and nests with *Crematogaster* ('*Physocrema*') *onusta* Stitz, 1925.

Literature. Itino & Yamane (1995), Tanaka et al. (2010).

Camponotus irritabilis (F. Smith, 1857) (sp. 5 of SKY) (Pl. 4: 19)

Collection data. 8 ha plot: w, 25.i.1993, SKY; w, 17.viii.1995, SKY; w, 4.xi.2001, foragers on flower, with *Crematogaster modiglianii*, A. Hatada. Around lab.: w, 2.viii.1995, SKY. HQ: 5.viii.1995, at night, SKY; w, 18.viii.1995, prey of *Odontoponera denticulata*, H. Okido. Tourist area: 25.i.1993, SKY; w, 15.viii.1997, at night, SKY; 22.iii.2013, shelter on tree stem, with *Cr. modiglianii*, SKY (Sr13-SKY-07).

Biology. Forest and forest edge; ground level to arboreal; nests in tree hollows; hunting live arthropods; mainly active in the night. This species shares foraging trails and nests with *Crematogaster* ('*Paracrema*') *modiglianii* Emery, 1900 (Yamane et al. 2018a).

Camponotus rufifemur Emery, 1900 (sp. 4 of SKY) (Pl. 4: 20)

Collection data. 8 ha plot: w, 20.viii.1995, SKY. HQ: w, 15–17.viii.1995, SKY. Tourist area: w, 25.i.1993, SKY; w, 6.viii.1995, night, SKY; w, 30.xii.1997, with *Crematogaster modiglianii*, SKY (SR97-SKY-109). 'Lambir': w, 20.viii.1995, Y. Hashimoto.

Biology. Forest; mainly arboreal; nests in big tree hollows; attracted to honeydew secreted by homopterans; mainly active during the night. This species shares foraging trails and nests with *Crematogaster* ('*Paracrema*') *modiglianii*.

Literature. Tanaka et al. (2007), Yamane et al. (2018a).

Camponotus sedulus (F. Smith, 1857) (sp. 64 of SKY)

Collection data. Bt. Lambir: w, 21.viii.1995, M. Kato.

Camponotus cf. winkleri Forel, 1911 (sp. 76 of SKY)

Collection data. Bt. Pantu: w, 13.viii.1995, SKY.

Subgenus *Tanaemyrmex* Ashmead, 1905

This includes large, slender and yellowish species, many of which are mainly nocturnal. They are highly polymorphic in the worker caste, and this causes many unsolved taxonomic problems. Many species are attracted to honeydew (Pl. 5: 23) and extrafloral nectary, and can be collected with sugar/honey bait trapping (Pl. 5: 24).

Camponotus arrogans (F. Smith, 1858) (sp. 7 of SKY)

Collection data. HQ: wq, 3-20.viii.1995, at night, SKY. 8 ha plot: w, 14.i.1993, at night, 35 m from ground on Tower I, SKY; w, 20.i.1993, honey bait, SKY (GN-3-30; TN-1-4); w, 20.i.1993, honey bait, SKY (GN-3-30; TN-1-4); w, 26.viii.1994, T. Itioka & T. Yumoto (#47); w, 15.viii.1995, ex epiphyte, SKY; w, 40.vi.2004, night, SKY. Around lab.: w, 2.viii.1995, SKY. Tourist area: w, 20.i.1993, SKY; w, 23.viii.1995, associated with bugs, SKY. Inoue trail: w, 2.vii.2004, SKY (SR04-SKY-73). Canopy 4 ha: w, 4.iii.2004, HOT (P3B2-2; P3B6-1, P3B8-1, P3B15-2); w, 7.iii.2004, HOT (P7B13-1); w, 8.iii.2004, HOT (P9B1). Bt. Pantu: w, 2.i.1998, F. Yamane. 50 ha plot: w, 12.i.1993, SKY. Bt Lambir: w, 12.i.1993, 400 m alt, SKY. ‘Lambir’: w, 15.v.2011, nest under moss cover nearby tree base, SKY (SR11-SKY-31); w, 16.v.2011, M. Ohashi (LL9-32, 10–30, A7, in soil); w, 12.i.2012, Y. Maekawa (LL10-11, 10–30, A4, in soil).

Biology. Forest; ground level to subcanopy; nests underground and in dead branches on live trees; attracted to extrafloral nectary, honeydew excreted by homopterans, and honey baits; generally nocturnal but occasionally lower activity seen during the daytime.

Literature. Itino & Yamane (1995), Yamane et al. (1996), Tanaka et al. (2010, 2012), Katayama et al. (2015; supporting information), Ohashi et al. (2017; nest CO₂ emission).

Camponotus carinifer Viehmeyer, 1916 (sp. 72 of SKY)

Collection data. 8 ha plot: w, 19.iv.1993, walkway 1, SKY; w, 30.vi.2004, cheese bait, SKY (SR04-SKY-60). 50 ha plot: w, 12.i.1993, SKY.

Biology. Forest; principally arboreal; attracted to cheese bait; active day and night.

Literature. Yamane et al. (1996), Tanaka et al. (2012).

Camponotus festinus (F. Smith, 1857) (sp. 12 of SKY)

Collection data. 8 ha plot: w, 25.viii.1995, attending bugs, SKY; w, 30.vi.2004, SKY (SR04-SKY-83). HQ: wq, 3–24.viii.1995, at light, SKY. Tourist area: w, 24.i.1993, night, SKY.

Biology. Forest; ground level to lower vegetation; attending homopterans and heteropterans for honeydew; new queens attracted to light.

Camponotus* cf. *setitibia Forel, 1901 (cf. sp. 54 of SKY)

Collection data. Canopy 4 ha: w, 7.iii.2004, dead twig at 24 m above ground, HOT (P7B13-1).

Biology. Forest; arboreal; nest in dead twig on tree.

Unidentified species in the subgenus *Tanaemyrmex*: **sp. 8 of SKY** (Tourist area), **sp. 13 of SKY** (8 ha plot, Inoue trail, Bt. Pantu; ground level to arboreal, nocturnal; SR04-SKY-68; Tanaka et al. 2012), **sp. 15 of SKY** (=sp. 73, 78 of SKY; 8 ha plot: forest, ground level to arboreal, attracted to honeydew excreted by homopterans and honey baits, pitfall trap, nocturnal; SR04-SKY-36; Yamane et al. 1996; Tanaka et al. 2007, 2010; Ohashi et al. 2017, nest CO₂ emission), **sp. 54 of SKY** (Canopy 4 ha; arboreal, nests in dead twigs; P1B3-1, P7B6, P7B12-2), **sp. 129 of SKY** (8 ha plot, Canopy 4 ha; arboreal, nests in dead twigs, AT0274-B, P8 B9, AT1455)

Taxonomic notes. *Camponotus* sp. 15 of SKY is a distinctive species with a deep orange or reddish head in the queen and major worker; the body is very hairy and the gaster bears very long hairs. It is rather common on the forest floor. Despite the easy recognition and common occurrence, we have not yet identified it.

Unidentified species in unknown subgenera of *Camponotus*: **sp. 41 of SKY** (50 ha plot; ‘Lambir’: AT0044, CN004; ant-mimic sample-016), **sp. 42 of SKY** (secondary forest nearby the national park), **sp. 93 of SKY** (from *Korthalsia rostrata*).

Genus *Colobopsis* Mayr, 1861

Named Bornean species: 13 (Pfeiffer et al. 2011, Laciny et al. 2018). Lambir species: 16 (6 named, 10 unidentified). The Lambir species are assigned to the following species groups: *C. cylindrica*-group (*cylindrica*, *leonardi*, *Camponotus* sp. 1b of SKY, *Camponotus* sp. 62 of SKY, *C. sp. 69 of SKY*, *explodens*, COCY-SKY-B, COCY-SKY-C, and COCY-SKY-D; last five belong to the *C. saundersi* (Emery 1889)-complex; Pl. 5: 22), *C. truncata*-group (*Camponotus* sp. 24 of SKY), *C. vitrea*-group (*vitrea*, *Camponotus* sp. 9 of SKY, sp. 38 of SKY), and unknown species groups (*macarangae*, *Camponotus* sp. 143 of SKY, sp. 177 of SKY). Taxonomy, morphology and biology of the *C. cylindrica*-group were studied by Laciny et al. (2017, 2018).

Colobopsis cylindrica (Fabricius, 1798) (*Camponotus* sp. 2 of SKY)

Collection data. 8 ha plot: w, 6.i.1993, 35 m from ground, SKY; w, 13.i.1993, walkway, SKY; w, 14.i.1993, Tower I at 35 m, night, SKY; w, 19.iv.1993, walkway, SKY; w, 25.viii.1993, sugar bait, T. Itino; w, 30.xii.1997, walkway, SKY. Tourist area: w, 20.i.1993, SKY; w, 1.iii.1997, SKY. ‘Lambir’: w, 4.vi.2001 (CR00006).

Biology. Forest; lower vegetation to canopy; attracted to sugar baits.

Literature. Itino & Yamane (1995).

Colobopsis exprodens Laciny et Zettel, 2018 (*Camponotus* sp. 1 of SKY, part)

Collection data. 8 ha plot: w, 6.i.1993, SKY; w, 7.i.1993, SKY; w, 11.i.1993, SKY; w, 13.i.1993, walkway, SKY; w, 21.i.1993, SKY; w, 18.iv.1993, SKY; w, 3.viii.1995, SKY; w, 25.viii.1993, canopy, sugar bait, T. Itino; w, 30.viii.1993, forest floor, sugar bait, T. Itino; w, 18.viii.1995, SKY; w, 19.viii.1996, SKY; w, 20.viii.1995, SKY; w, 23–24.viii.1995, Tower II, SKY; w, 3.viii.1997, walkway, SKY; w, 17.viii.1997; w, 30.xii.1997, SKY. Tourist area: w, 25.i.1993, SKY; w, 1.iii.1997, SKY.

Biology. Forest; lower vegetation to canopy; attracted to sugar and cheese baits but only occasionally. Foragers sometimes accepted dead insects but we never witnessed transportation of the ‘prey’ to their nests (Hashimoto et al. 1997).

Literature. Itino & Yamane (1995; as *Camponotus saundersi*), Hashimoto et al. (1997; as *Camponotus saundersi*), Tanaka et al. (2007), Katayama et al. (2015; supporting information).

Colobopsis leonardi Emery, 1889 (*Camponotus* sp. 3 of SKY)

Collection data. 8 ha plot: w, 28.v.1993, canopy, sugar bait, T. Itino; w, 27.viii.1994, T. Itioka & T. Yumoto (#68). HQ: fq, 13–14.i.1993, at light, SKY. Bt. Lambir: 12.i.1993, SKY.

Taxonomic notes. This may be a species-complex comprising several cryptic species. The specimens from Lambir have the gastral pilosity sparser than in those from mainland Asia (Thailand and Vietnam).

Biology. Forest; lower vegetation to canopy; nests in dead branches; attracted to extrafloral nectary and sugar baits; winged queens attracted to light; active in the daytime.

Literature. Itino & Yamane (1995), Tanaka et al. (2010, 2012), Katayama et al. (2015; supporting information).

Colobopsis macaranga (DumPERT, 1996) (*Camponotus* sp. 166 of SKY)

Collection data. Bt. Pantu: w & fq, 23.iii.2013, ex *Macaranga lamellata*, SKY (SR13-SKY-25). ‘Lambir’: w & wq, iii.1996, T. Itino (TI-96-03).

Biology. This species is a partner of *Macaranga lamellata*, living in its hollow stems.

Literature. DumPERT (1996).

Colobopsis vitrea (F. Smith, 1860) (*Camponotus* sp. 14 of SKY)

Collection data. 8 ha plot: w, 6.i.1993, 35 m high on tree, SKY; 14.i.1993, Tower I, 35 m, night, SKY; w, 30.viii.1993, 35 m from ground, sugar bait, T. Itino; w, 27.viii.1994, T. Itioka & T. Yumoto (#87); w, 24–24.viii.1995, Tower II–walkway, SKY. Bt. Pantu: 16.i.1993, SKY; 2.i.1998, F. Yamane.

Biology. Forest; arboreal; attracted to sugar baits; active day and night.

Literature. Itino & Yamane (1995).

Unidentified species in *Colobopsis* (*Camponotus* is still used for species codes):

***Camponotus* sp. 1b of SKY** (*C. cylindrica*-group; 8 ha plot, Inoue trail: SR04-SKY-76), Bt. Pantu, Tourist area, 50 ha plot, Bt. Lambir), ***Camponotus* sp. 9 of SKY** (*C. vitrea*-group; 8 ha plot: arboreal, active in the daytime; AT1238; ‘Lambir’: ex *Macaranga* TK960012; Yamane et al. 1996; Katayama et al. 2015, supporting information), ***Camponotus* sp. 28 of SKY** (*C. truncata*-group; 8 ha plot; arboreal, active at night; wq, AT0122; w, AT0138), ***Camponotus* sp. 38 of SKY** (*C. vitrea*-group; 8 ha plot; Canopy 4 ha: P6 B9-2, P10 B9, nests in dead twigs at 25.4 m above ground; Tanaka et al. 2012), ***Camponotus* sp. 62 of SKY** (*leonardi*-complex in *C. cylindrica*-group; 8 ha plot: walkway), ***Camponotus* sp. 69 of SKY** (*leonardi*-complex in *C. cylindrica*-group; 8 ha

plot, Bt. Pantu; lower vegetation to canopy, attracted to extrafloral nectary and sugar baits; Tanaka et al. 2010, 2012; Katayama et al. 2015, supporting information), ***Camponotus* sp. 143 of SKY** (= *C. 155 of SKY*; Canopy 4 ha: w & m; ant-mimic-sample-191; CN008, canopy; Katayama et al. 2015, supporting information), ***Camponotus* sp. 177 of SKY** (wq, HQ, at light), **sp. COCY-SKY-B** (*C. cylindrica*-group, = *Camponotus* sp. 1b; 8 ha plot, 50 ha plot, 'Lambir'), **sp. COCY-SKY-C** (*C. cylindrica*-group; 8 ha plot, 'Lambir'), **sp. COCY-SKY-D** (*C. cylindrica*-group; 8 ha plot, Sungai Liku, 'Lambir'; *Shorea* seedling EFN).

Genus *Dinomyrmex* Ashmead, 1905

Named Bornean species: 1 (Pfeiffer et al. 2011, as species of *Camponotus*). Lambir species: 1 (named).

Dinomyrmex gigas (Latreille, 1802) (sp. 1 of SKY; = *Camponotus* sp. 87 of SKY) (Pl. 5: 25, 26; Pl. 6: 27, 28)

Collection data. 8 ha plot: w, 12.i.1993, honey bait, SKY; w, 14.i.1993, Tree Tower I, 16 m above ground, at night, SKY. Tourist area: w, 31.xii.1997, SKY; w, 1.i.1998, SKY. HQ: m, 3–24.viii.1995, at light, SKY. Bt. Lambir: w, 13–14.viii.1995, Kerangas forest, J. Otsubo.

Biology. Forest; ground level, also foraging on trees including canopy; nest in decayed wood and soil; carnivorous, even attacking small reptiles (Pl. 5: 25); collecting mushroom; attracted to *Endospermum* EFN, and honey and cheese baits; males attracted to light; active day and night. Foragers are generally solitary during the daytime, but in groups during the night. Fierce battles are often seen between different colonies, leaving numerous corpses on the ground. The behavior of this species was studied in Sabah by Pfeiffer & Linsenmair (2000). According to them most nests were polydomous, dug in soil; one colony had eleven nests, a territory of 0.8 ha and around 7,000 workers. A fungus parasitizes adult workers of this ant (Pl. 5: 26).

Literature. Itino & Yamane (1995), Yamane et al. (1996), Hashimoto et al. (1997), Tanaka et al. (2010, 2012), Ohashi et al. (2017; nest CO₂ emission).

Genus *Echinopla* F. Smith, 1857

Named Bornean species: 12 (Pfeiffer et al. 2011; Zettel & Laciny 2015, 2017). Lambir species: 7 (3 named, 4 unidentified).

Echinopla melanarctos F. Smith, 1857 (sp. 1 of SKY)

Collection data. 8 ha plot: w, 16.xii.1993, Abd. Rahman Nona.

Echinopla mezgeri Zettel et Laciny, 2015 (sp. 11 of SKY)

Collection data. 'Lambir': 15.viii.1997, SKY.

Echinopla striata F. Smith, 1857 (sp. 4 of SKY)

Collection data. 8 ha plot: w, 17.ix.2004, HOT (AT0570). Canopy 4 ha: w, 2.vii.2004,

SKY (AT0273).

Biology. Forest; principally arboreal; nest in dead twigs.

Unidentified species in *Echinopla*: **sp. 5 of SKY** (HQ), **sp. 12 of SKY** (8 ha plot: arboreal), **sp. 16 of SKY** (Canopy 4 ha; forest, arboreal, nests in dead twigs; DUA001, P3B7, P2B9-1; Katayama et al. 2015, supporting information), **sp. 20 of SKY** (8 ha plot; arboreal; AT1137).

Genus *Polyrhachis* F. Smith, 1857

Named Bornean species: 105 (+ 4 subspecies; Pfeiffer et al. 2011, Kohout 2013). Lambir species: 57 (32 named, 25 unidentified). *Polyrhachis* species are dominant components of the ant fauna on trees and in canopies (e.g., Katayama et al. 2015). However, their biology has been poorly clarified. Some species are models for ant-mimicking spiders of the genus *Sphecotypus* and *Myrmarachne* (e.g., Yamasaki et al. 2017, Hashimoto et al. 2020).

Subgenus *Campomyrma* Wheeler, 1911

Polyrhachis equina F. Smith, 1857 (sp. 133 of SKY)

Collection data. 8 ha plot: w, 23.i.1993, SKY; w, 6.viii.1995, SKY; w, 19–21.viii.1995, pitfall trap, J. Otsubo.

Biology. Forest; mainly ground surface.

Subgenus *Chariomyrma* Forel, 1915

Polyrhachis arcuata (Le Guillou, 1842) (sp. 52 of SKY)

Collection data. ‘Lambir’: w, 10.viii.1995, forest edge, SKY.

Biology. Forest edge; lower vegetation.

Subgenus *Cyrtomyrma* Forel, 1915

Polyrhachis danum Kohout, 2006 (sp. 41 of SKY)

Collection data. ‘Lambir’: w, 21–27.ii.2009 (ant-mimic sample<09F246-1>).

Polyrhachis lepida Kohout, 2006 (sp. 162 of SKY)

Collection data. 8 ha plot: w, 3.iii.1997, walkway 1–4, SKY; w, 29.ix.2006, HOT (AT1367, AT1384). HQ: 25.viii.1995, SKY.

Biology. Forest; arboreal.

Subgenus *Hemioptica* Roger, 1862

Polyrhachis boltoni Dorow et Kohout, 1995 (sp. 104 of SKY)

Collection data. 8 ha plot: fq, 3.iii.1995, SKY; w, 11.viii.1995, SKY; 3.iii.1997, SKY. Sungai Liku: w, 23.iii.2013, Shorea seedling EFN, SKY.

Biology. Forest; lower vegetation; attracted to extrafloral nectary.

Subgenus *Myrma* Billberg, 1820

Polyrhachis hosei Donisthorpe, 1942 (sp. 53 of SKY)

Collection data. HQ: w, 3.viii.1995, H. Okido.

Polyrhachis illaudata Walker, 1859 (sp. 107 of SKY)

Collection data. 8 ha plot: w, 13.i.1993, SKY; w, 23.i.1993, SKY; w, 26.i.1993, SKY; w, 31.i.1993, sugar bait, SKY. HQ: w, viii.1995, SKY. Tourist area: fq, 24.i.1993, at night, SKY.

Taxonomic notes. This species is highly variable in morphology, especially in the shape of the petiole and its spines, and probably represents a species-complex.

Biology. Forest; lower vegetation to arboreal; attracted to sugar baits.

Literature. Yamane et al. (1996; as *P. tyrannica*), Katayama et al. (2015; supporting information).

Polyrhachis inermis F. Smith, 1858 (sp. 166 of SKY, part)

Collection data. 8 ha plot: w, 6.i.1993, SKY (det. as *P. orsylla* by R. Kohout); w, 22.i.1993, SKY; w, 30.i.1993, SKY; w, 31.i.1993, SKY; w, 21.viii.1995, SKY. Bt. Pantu: 2.i.1998, F. Yamane. Tourist area: w, 1.i.1998, SKY. ‘Lambir’: w, 14.v.2011, SKY.

Taxonomic notes. *Polyrhachis inermis*, *P. orsylla* F. Smith, 1861 and *P. vindex* F. Smith, 1857, all belonging to the *P. inermis*-group, are very similar to each other. *P. inermis* has an entirely black body, while in *P. vindex* the legs are extensively reddish to yellowish brown (but intermediate individuals are occasionally found). Lambir apparently lacks *P. orsylla*, in which the sculpture of the head and pronotal dorsum is said to be much finer than in *P. vindex* (see Kohout 1998).

Biology. Forest; lower vegetation; attracted to honeydew excreted by homopterans.

Polyrhachis nigropilosa Mayr, 1872 (sp. 9 of SKY)

Collection data. 8 ha plot: w, 20.i.1993, sugar bait, night, SKY; w, 20.viii.1994, T. Itioka & T. Yumoto (#49); w, 13.v.2011, SKY. Tourist area: w, 20.i.1993, SKY; w, 25.i.1993, SKY; w, 2.i.1998, SKY. 50 ha plot: w, 24.iii.2013, SKY. Secondary forest nearby the national park: w, 26.vi.2004, SKY.

Biology. Forest; mainly ground level; attracted to sugar baits; active day and night.

Literature. Yamane et al. (1996), Hashimoto & Yamane (2014; prey of army ants).

Polyrhachis striata Mayr, 1862 (sp. 32 of SKY)

Collection data. 8 ha plot: w, 20.viii.1995, SKY.

Polyrhachis* cf. *striatorugosa Mayr, 1862 (sp. 12 of SKY; =sp. 31, sp. 116 of SKY)

Collection data. 8 ha plot: w, 26.viii.1994, T. Itioka & T. Yumoto (#35); w, 27.viii.1994, same collectors (#121); w, 30.vi.2004, at night, SKY; w, 2.x.2004, HOT (AT1454, 1506). Tourist area: 24.i.1993, at night, SKY. ‘Lambir’: w, 14–19.viii.1997, SKY.

Taxonomic notes. According to R. Kohout (personal communication) this species is closely related to *P. striatorugosa* described from Java, but differs from the latter in

having a much finer sculpturation on the head and mesosoma.

Biology. Forest; lower vegetation to arboreal; foragers often found in the night.

Polyrhachis subpilosa Emery, 1895 (sp. 62 of SKY)

Collection data. 8 ha plot: w, 2–9.xii.2012 (ant-mimic sample<20121209-E103G>).

Taxonomic notes. R. Kohout (personal communication) suggested that this species might be a junior synonym of *P. zophyra edentula* Emery, 1900 (*P. zophyra*-group).

Polyrhachis vindex F. Smith, 1857 (sp. 124 of SKY)

Collection data. 8 ha plot: w, 2.viii.1995, SKY; w, 16.viii.1995, SKY; w, 30.xii.1997 (SKY). Tourist area: w, 30.xii.1997, SKY.

Biology. Forest; lower vegetation; attracted to honeydew excreted by homopterans.

Literature. Tanaka et al. (2007).

Unidentified species in the subgenus *Myrma*: **sp. 10 of SKY** (close to *P. striata*; 8 ha plot, 50 ha plot, Bt. Lambir; arboreal; Itino & Yamane 1995), **sp. 11 of SKY** (*P. villipes* group; 8 ha plot, 50 ha plot, Bt. Lambir), **sp. 13 of SKY** (8 ha plot), **sp. 193 of SKY** (close to *P. murina* Emery, 1893; ant-mimic sample, 20121209-H80G).

Subgenus *Myrmatopa* Forel, 1915

Polyrhachis flavicornis F. Smith, 1857 (sp. 129 of SKY; =sp. 144 of SKY)

Collection data. ‘Lambir’: w, 21–27.ii.2009 (ant-mimic sample, 09F245).

Literature. Katayama et al. (2015; supporting information).

Polyrhachis jacobsoni Forel, 1909 (sp. 87 of SKY)

Collection data. 8 ha plot: w, wq & m, 28.ix.2006, HOT (AT1366).

Biology. Forest; arboreal.

Unidentified species in the subgenus *Myrmatopa*: **sp. cf. 46 of SKY** (AT1502), **sp. 55 of SKY** (‘Lambir’, CN049), **sp. 61 of SKY** (*P. wallacei*-group; ‘Lambir’), **sp. 172 of SKY** (‘Lambir’; forest, at night), **sp. 174 of SKY** (8 ha plot; nest in space formed of leaves woven with silk, active at night; HT03-0735).

Subgenus *Myrmhopla* Forel, 1915

Polyrhachis abdominalis F. Smith, 1858 (sp. 81 of SKY) (Pl. 7: 29)

Collection data. 8 ha plot: w, 30.viii.1993, on tree, sugar bait, T. Itino; w, 3.viii.1995, SKY. HQ: w, 3–20.viii.1995, SKY.

Biology. Forest and forest edge; lower vegetation to arboreal; nests in tree hollows; attracted to sugar baits.

Literature. Itino & Yamane (1995), Tanaka et al. (2012).

Polyrhachis armata (Le Guillou, 1842) (sp. 2 of SKY) (Pl. 7: 33)

Collection data. 8 ha plot: w, 13.i.1993, SKY; w, 14.i.1993, SKY; w, 18.iv.1993, SKY; w, 25.viii.1993, canopy, sugar bait, T. Itino; w, 25.viii.1993, bush, T. Itino; w, 30.xii.1993, walkway, SKY; w, 3.viii.1995, SKY. HQ: wq, 3–24.1995, at light, SKY.

Tourist area: w, 20.i.1993, SKY; w, 30.i.1993, SKY. Bt. Pantu: w, 16.i.1993, SKY. 50 ha plot: w, 7.i.1993, SKY; w, 27.i.1993, SKY. Bt. Lambir: 12.i.1993, SKY.

Biology. Forest; lower vegetation to arboreal; attracted to extrafloral nectary and sugar baits; winged queen at light.

Literature. Itino & Yamane (1995), Tanaka et al. (2007, 2012), Yamasaki et al. (2017; model of a spider, *Sphecotypus borneensis* Yamasaki).

Polyrhachis basirufa Emery, 1900 (sp. 74 of SKY)

Collection data. 8 ha plot: w, 23–24.viii.1995, Tower 2–walkway, SKY; w, Bt. Pantu, 2.i.1998, F. Yamane.

Biology. Forest; arboreal.

Polyrhachis bicolor F. Smith, 1858 (sp. 7 of SKY)

Collection data. HQ: 2.iii.1997, SKY (SR97-SKY-01). Tourist area: w, 30.xii.1997, SKY; w, 1.i.1998, SKY. ‘Lambir’: w, 6.iv.2010, Kishimoto & Itioka (CN250).

Biology. Forest edge, disturbed area; arboreal; attracted to sugar baits; active in the daytime.

Literature. Katayama et al. (2015; supporting information).

Polyrhachis caeciliae Forel, 1912 (sp. 57 of SKY)

Collection data. ‘Lambir’: w, 30.x.1996, Y. Hashimoto.

Polyrhachis calypso Forel, 1911 (sp. 3 of SKY)

Collection data. HQ: wq, 3–24.viii.1995, at light, SKY. Bt. Lambir: w, 13–14.1995, 200 m alt., SKY.

Biology. Forest; lower vegetation; winged queen attracted to light.

Polyrhachis chalybea F. Smith, 1857 (sp. 80 of SKY)

Collection data. 8 ha plot: w, 19.iv.1993, walkway, SKY. Bt. Lambir: 12.i.1993, >450 m alt., SKY. ‘Lambir’: 30.x.1996, Y. Hashimoto.

Biology. Forest; lower vegetation to arboreal; nest under bark of living tree; active in the daytime.

Literature. Tanaka et al. (2012).

Polyrhachis* cf. *chrysophanes Emery, 1900 (sp. 23 of SKY)

Collection data. 8 ha plot: w, 3.iii.1997, SKY; w, vi–viii.2004, HOT & T. Itioka (DAT637).

Biology. Forest; lower vegetation to arboreal; active in the daytime.

Polyrhachis cryptoceroides Emery, 1887 (sp. 68 of SKY)

Collection data. 8 ha plot: w, xii.2003–iii.2004, HOT (#DAT386); 14.vii.2010, HOT (CA1205).

Biology. Forest; arboreal; nests in aerial soil accumulated at branch forks; active in the daytime.

Literature. Tanaka et al. (2012).

Polyrhachis dives F. Smith, 1857 (sp. 72 of SKY)

Collection data. 8 ha plot: w, 10.xii.1993, SKY.

Polyrhachis flavoflagellata Karavaiev, 1927

Collection data. 8 ha plot: w, 14.i.1993, Tower 1 at 35 m above ground, SKY; xii.2003–iii.2004, HOT & T. Itioka (DAT241); w, 21.ix.2006, HOT (AT1249).

Biology. Forest; arboreal.

Polyrhachis furcata F. Smith, 1858 (sp. 1 of SKY)

Collection data. 8 ha plot: w & fq, viii.1995, SKY (95-L-01); w, 3.i.1998, SKY. ‘Lambir’: w, 2.i.1998, SKY.

Biology. The nest 95-L-01 was found on a small tree (1.8 m high). It was an initial colony comprising a foundress and several very small workers. The nest made of fine pulp pieces was located in a rolled leaf that was lined inside with silk.

Polyrhachis hector F. Smith, 1857 (sp. 78 of SKY)

Collection data. 8 ha plot: w, 6.i.1993, 16 m above ground, SKY; w, 19.iv.1993, tree tower, 20 m above ground, SKY. HQ: w, 25.viii.1995, SKY (L-95-30). Tourist area: w, 30.i.1993.

Biology. Forest, forest edge; arboreal; nest in compartmentalized space under bark and in cavity formed of leaves woven with silk; active in the daytime.

Literature. Tanaka et al. (2010, 2012).

Polyrhachis muelleri Forel, 1893 (sp. 40 of SKY)

Collection data. Tourist area: w, 23.viii.1995, SKY.

Biology. Forest; lower vegetation.

Polyrhachis cf. personata Wheeler, 1919 (sp. 4 of SKY; =*sp. 16 of SKY*) (Pl. 7: 31)

Collection data. 8 ha plot: w, 3.viii.1995, SKY (95-L-02); w, 23–24.viii.1995, walkway, SKY. 50 ha plot: 12.i.1993, SKY.

Biology. Forest; arboreal; active in the daytime. The nest 95-L-02 was found in a rolled live leaf, with a larva and cocoons. Since the foundress, eggs and young larvae were absent, this might have been a part of the colony.

Literature. Tanaka et al. (2012).

Polyrhachis rufipes F. Smith, 1858 (sp. 44 of SKY)

Collection data. 8 ha plot: w, 21.viii.1995, SKY; w, 3.i.1998, F. Yamane.

Biology. Forest; lower vegetation. Foragers are often found together with *Gnamptogenys menadensis* workers on plant leaves; these are similar to each other in coloration.

Polyrhachis storki Kohout, 2008 (sp. 141 of SKY)

Collection data. 8 ha plot: w & m, 11.ix.2005, HOT (AT1058). ‘Lambir’: w, 7.vi.2001 (CR00047); w, 21.vi.2005 (ISO0185).

Taxonomic notes. This species belongs to the *P. flavoflagellata*-group and is distinguished from *P. flavoflagellata* by the deeply emarginated anterior clypeal margin in *P. storki* (Kohout 2008).

Polyrhachis cf. tibialis F. Smith, 1858 (sp. 6 of SKY; ?=*sp. 66*)

Collection data. Typical form. ‘Lambir’: w, 3.viii.2001 (CR00070). Variety

‘*caligata*’. ‘Lambir’: w, 10.viii.1995, forest edge, SKY; w, 16.ix.2009, Kishimoto & Itioka (CN093); w, 26.ix.2009, Kishimoto & Itioka (CN070).

Taxonomic notes. This belongs to the *P. saevissima* F. Smith-group. R. Kohout (personal communication) suggested that the specimens from Lambir resemble *P. tibialis* originally described from Myanmar but that some differences exist between the Lambir specimens and those from Myanmar. The variety *caligata* Emery, 1895 (also described from Myanmar) has the mid- and hind-tibiae extensively reddish brown, while in the typical form the mid- and hind-tibiae are entirely black.

Biology. Forest edge; lower vegetation to arboreal; nest in aerial soil accumulated at base of epiphytes; active in the daytime.

Literature. Katayama et al. (2015; supporting information).

***Polyrhachis* cf. *wheeleri* Mann, 1919 (sp. 16 of SKY)**

Collection data. Inoue trail: w, 2.vii.2004, SKY. Tourist area: w, 31.xii.1997, SKY.

Unidentified species in the subgenus *Myrmhopla*: **sp. 20 of SKY** (*P. bicolor*-group; 8 ha plot; forest, arboreal; ‘Lambir’, CN266; Katayama et al., 2015, supporting information), **sp. 48 of SKY** (8 ha plot, ex epiphyte), **sp. 142 of SKY** (8 ha plot; lower vegetation to arboreal, attracted to extrafloral nectary; Tanaka et al. 2007, 2012), **sp. 143 of SKY** (*P. saevissima*-group; 8 ha plot; arboreal; DAT 150; Katayama et al. 2015, supporting information), **sp. 155 of SKY** (8 ha: AT1083), **sp. 198 of SKY** (*P. mucronata* group; 8 ha plot, Bt. Pantu, Tourist area; lower vegetation, attracted to extrafloral nectary; Tanaka et al. 2007, as *P. phalerata*), **sp. 203 of SKY** (CN007-158).

Subgenus *Myrmothrinax* Forel, 1915

***Polyrhachis* cf. *textor brunneogaster* Donisthorpe, 1937 (sp. 59 of SKY)**

Collection data. Tourist area: w, 19.viii.1997, SKY.

Taxonomic notes. *Polyrhachis* sp. 95 of SKY collected in HQ at light are possibly winged queens of this species.

***Polyrhachis* cf. *thrinax* Roger, 1863 (sp. 60 of SKY)**

Collection data. HQ: wq, 3–24.viii.1995, at light, SKY. ‘Lambir’: wq, 14–19.viii.1997, SKY.

Biology. Queens are attracted to light.

***Polyrhachis triaena* Wheeler, 1919 (sp. 93 of SKY)**

Collection data. HQ: wq, 3–24.viii.1995, at light, SKY.

Unidentified species in the subgenus *Myrmothrinax*: **sp. 45 of SKY** (HQ, 8 ha plot; arboreal, nest in space formed of leaves woven with silk, AT1092; ant-mimic sample 13-1; TY-10-04), **sp. 154 of SKY** (8 ha plot; arboreal, nest in space formed of leaves woven with silk, active at night; AT0212).

Subgenus *Polyrhachis* F. Smith, 1857

Polyrhachis bihamata Drury, 1773 (sp. 84 of SKY) (Pl. 7: 30)

Collection data. 8 ha plot: w, 13.i.1993, SKY; w, 17.viii.1995, SKY.

Biology. Forest; arboreal for foraging, but also seen on ground surface; nest in soil; attracted to honey and cheese baits. A nest was found in soil with the entrance near the base of a tree. Dead insects were accepted by workers, although it is not known if they are used as larval food. Most items carried back to the nest were not identified (resin-like sticky material, transparent sticky balls, seemingly plant tissue etc.) (personal observations by SKY and Y. Hashimoto). An ant-mimicking spider, *Corinnomma* sp. (Corinnidae), was seen close to the nest, mixed with ant foragers that were cautious of the spider (Pl. 7: 32).

Literature. Hashimoto et al. (1997).

Polyrhachis olybria Forel, 1912 (sp. 82 of SKY)

Collection data. 8 ha plot: w, 7–21.i.1993, SKY; w, 25.viii.1993, canopy, sugar bait, T. Itino; w, 27.viii.1994, T. Itioka & T. Itino (#60); w, 30.xii.1997, SKY. ‘Lambir’: 2.vi.1994, T. Nagamitsu.

Taxonomic notes. This species had been treated as *P. belicosa* (F. Smith, 1859) until Kohout (2014) reviewed the subgenus *Polyrhachis* (e.g., Yamane & Nona 1994).

Biology. Forest; arboreal; attracted to extrafloral nectary and sugar baits.

Literature. Itino & Yamane (1995; as *P. belicosa*).

Tribe Lasiini Ashmead, 1905

Genus *Cladomyrma* Wheeler, 1920

Named Bornean species: 11 (Pfeiffer et al. 2011). Lambir species: 4 (3 named, 1 unidentified). All species of this genus live in stems of live plants.

Cladomyrma andrei (Emery, 1894) (sp. 7 of SKY)

Collection data. 8 ha plot: w, v–vi.2003, HOT & T. Itioka (#HOT03-0364), w & fq, xii.2003, HOT & T. Itioka (#DAT 004–006). Secondary forest nearby the national park: w, 26.vi.2004, Fabaceae climber, SKY (SR04-SKY-07).

Biology. Forest; arboreal; attracted to extrafloral nectary. This is a plant-ant species, which inhabits in a climber, *Spatholobus* sp., of the bean family (Fabaceae), and lives together with coccoids in hollowed twigs of the ant-plant.

Literature. Tanaka et al. (2007).

Cladomyrma crypteroniae Agosti, Moog et Maschwitz, 1999 (sp. 4 of SKY)

Collection data. Tourist area: w, 14.viii.1995, M. Kato. ‘Lambir’: w, 4.viii.1995, Y. Hashimoto (M95080408).

Cladomyrma hobbyi Donisthorpe, 1937 (sp. 2 of SKY)

Collection data. 8 ha plot: w, 20.viii.1994, T. Itioka (#131, 132). Secondary forest nearby the national park: w, 26.viii.2003, HOT (LUB03-03418, -03365, -03435); w,

fq & m, 16.ix.2003, HOT (BTA1757, 1957); w, 26.vi.2004, Fabaceae climber, SKY (SR04-SKY-02), w & m, same date & plant, SKY (SR04-SKY-05); w & m, same date & plant, SKY (SR04-SKY-06); w & m, same date and plant, SKY (SR04-SKY-08); w & fq, 26.vi.2004, Fabaceae climber, HOT. 'Lambir': fq, 5.i.2002, C. Yoneyama (SPA 53-JNT-5); w, 14.i.2002, C. Yoneyama (ANA 5-1); fq, 25.i.2002, C. Yoneyama (ANA 10) .

Biology. Forest; lower vegetation to subcanopy; attracted to extrafloral nectary. A plant-ant species, which inhabits the stem of a climber, *Spatholobus* sp., of the bean family (Fabaceae) from the ground level to subcanopy up to 24 m above ground. This species lives together with coccoids in hollowed twigs of the climber. It is often found with *Crematogaster* cf. *cylindriceps* Wheeler, 1927 in the secondary forest, and with *Tetraponera inversinodis* Ward, 2001 and *T. pilosa* F. Smith, 1858 in the subcanopy of the 8 ha plot, in the same plants but from different nodes (Yamane et al. 2018a, p. 193).

Literature. Yamane et al. (2011, 2018a).

Cladomyrma* cf. *nudidorsalis Agosti, Moog et Maschwitz, 1999 (sp. 10 of SKY)

Collection data. Fragmented primeval forest nearby the national park: w & fq, 16.ix.2003, HOT (BTA1841).

Biology. Forest; lower vegetation. A plant-ant species, which inhabits the stem of a myrmecophytic species of the bean family (Fabaceae), living together with coccoids in hollowed twigs of the ant-plant.

Genus *Euprenolepis* Emery, 1906

Named Bornean species: 7 (LaPolla 2009, Pfeiffer et al. 2011). Lambir species: 3 (named). Lambir apparently lacks the most common species, *E. procera* (Emery, 1900).

Euprenolepis* *thrix LaPolla, 2009 (sp. 7 of SKY)

Collection data. 'Lambir': w, 21–27.ii.2009 (ant-mimic sample 090222-016).

Euprenolepis* *variegata LaPolla, 2009 (sp. 6 of SKY)

Collection data. 'Lambir': w, 15.vi.2011, Y. Maekawa (LC 57).

Biology. Forest; ground level; nest in soil.

Literature. Ohashi et al. (2017; nest CO₂ emission).

****Euprenolepis* *wittei*** LaPolla, 2009 (sp. 1 of SKY)

Collection data. 8 ha plot: w, 16.viii.1995, nest in soil, SKY (95-L-08). 50 ha plot: w, 24.iii.2013, SKY.

Biology. Forest; ground level; nest in soil.

Genus *Gesomyrmex* Mayr, 1868

Named Bornean species: 1 (Pfeiffer et al. 2011). Lambir species: 1 (named).

Gesomyrmex* *chaperi André, 1892 (sp. 1 of SKY)

Collection data. 8 ha plot: w, 4.viii.2004, HOT (Canopy 04-00228).

Biology. Forest; arboreal; active in the daytime.

Genus *Nylanderia* Emery, 1906

Named Bornean species: 2 (Pfeiffer et al. 2011). Lambir species: 7 (all unidentified). This is taxonomically one of the most difficult groups. No revision nor key for Southeast Asian species is available. All the Lambir species were collected from the ground level.

Unidentified species in *Nylanderia*: **sp. 1 of SKY** (= *Paratrechina* sp. 8 of SKY; 8 ha plot, Tourist area, 50 ha plot; ground level to lower vegetation, active in the daytime; Tanaka et al. 2010; Ohashi et al., 2017: nest CO₂ emission), **sp. 6 of SKY** (8 ha plot; ground level to arboreal, nest in aerial soil accumulated at branch forks and epiphytes, attracted to *Endospermum* EFN and honey baits on ground, active day and night; Yamane et al. 1996, Tanaka et al. 2010, 2012; Ohashi et al. 2017; nest CO₂ emission), **sp. 13 of SKY** (= *Paratrechina* sp. 3 of SKY; 8 ha plot), **cf. sp. 15 of SKY** ('Lambir': ISO0222), **sp. 18 of SKY** (= *Paratrechina* sp. 9 of SKY; 8 ha plot: attracted to *Endospermum* EFN and sugar baits on ground), **sp. 23 of SKY** (= *Paratrechina* sp. 5 of SKY; 8 ha plot, Tourist area, 50 ha plot, 'Lambir': forest floor, attracted to *Endospermum* EFN; SQ-1045, 1157), **sp. 25 of SKY** (= *Paratrechina* sp. 41 of SKY; 8 ha plot; Inoue trail: nest in rotting wood, SR04-SKY-69; nest in sandy soil, SR04-SKY-77; Tourist area: nest in rotting wood, SR04-SKY-31; 'Lambir': many workers ex soil).

Genus *Paraparatrechina* Donisthorpe, 1947

Named Bornean species: 2 (Pfeiffer et al. 2011). Lambir species: 8 (3 named, 5 unidentified). Until recently species of this genus have been placed in the genus *Paratrechina*. As no key to Asian species is available, the identification of species is extremely difficult.

Paraparatrechina butteli (Forel, 1913) (sp. 4 of SKY; = *Paratrechina* sp. 31 of SKY, *P. sp. 1 of SKY* part)

Collection data. 8 ha plot: w, 7.i.1993, SKY; w, 11.i.1993, SKY; w, 13.i.1993, attracted to sugar bait, night, SKY (GN-2-14); w, xii.2003–iii.2004, HOT (DAT398). Bt. Pantu: w, 16.i.1993, SKY. Tourist area: w, 24.i.1993, SKY. 'Lambir': w, 6.x.2013, forest floor, Kitora & Itioka (SQ1130).

Biology. Forest; ground level; attracted to honey baits; active in the night.

Literature. Yamane et al. (1996).

Paraparatrechina opaca (Emery, 1887) (sp. 1 of SKY, = *Paratrechina* sp. 1 of SKY)

Collection data. 8 ha plot: w, 6.i.1993, SKY; w, 11.i.1993, SKY; w, 14.i.1993, SKY; w, 23.i.1993, SKY; w, 26.i.1993, SKY; w, 3.viii.1995, SKY. Tourist area: w, 2.1.1998, SKY. 50 ha plot: w, 27.i.1993. Bt. Lambir: w, 12.i.1993, 400 m alt., SKY.

Taxonomic notes. This species is very similar to *P. butteli* in body shape, proportion, sculpture and color. The distinction between them was tentatively done by Cephalic

Index (head width/head length). This species has a shorter head ($CI > 0.8$; generally > 0.85), while *P. butteli* has a longer head ($CI < 0.8$). These two are separable from the related mountain species *P. emarginata* (Forel, 1913) by weaker body sculpture and smooth propodeal declivity (in the latter entire body tightly and strongly punctate and propodeal declivity transversely striate).

Biology. Forest; ground level to arboreal; attracted to extrafloral nectary and honeydew excreted by homopterans.

Literature. Tanaka et al. (2007).

**Paraparatrechina tapinomoides* (Forel, 1905) (sp. 7 of SKY; =*Paratrechina* sp. 4)

Collection data. 8 ha plot: w, 21.i.1993, SKY; w, 30.i.1993, sugar bait, SKY; w, 31.i.1993, honey bait, SKY; w, xii.2003–iii.2004, HOT.

Taxonomic notes. The present material was identified by its peculiar color pattern (dorsa of mesosoma and gaster yellowish; antenna and legs entirely yellow) mentioned in the original description by Forel (1905).

Biology. Forest; ground level to arboreal; attracted to *Endospermum* EFN, and honey and cheese baits.

Literature. Yamane et al. (1996).

Unidentified species in *Paraparatrechina*: **sp. 2 of SKY** (= *Paratrechina* sp. 2 of SKY; HQ, Tourist area), **sp. 6 of SKY** (= *Paratrechina* sp. 42 of SKY; 8 ha plot, Canopy 4 ha, 50 ha plot), **sp. 8 of SKY** (= *Paratrechina* sp. 24 of SKY; 8 ha plot; arboreal; AT1287, AT1105), **sp. 9 of SKY** (= *Paratrechina* sp. 12 of SKY; Canopy 4 ha; arboreal; nest in dead twig; P3B15-1, AT0475; ‘Lambir’: prey of *Aenictus*, BOTY500B, **sp. 10 of SKY** (= *Paratrechina* sp. 40 of SKY; 8 ha plot: DAT146; Canopy 4 ha: arboreal, nest in dead twig, P10B8-1).

Genus *Paratrechina* Motschoulsky, 1863

Paratrechina longicornis (Latreille, 1802) (sp. 1 of SKY)

Collection data. HQ: w, 7.i.1993, SKY; w, 1–3.iii.1997, SKY. ‘Lambir’: w & fq, 3.vii.1998, M. Arakawa.

Biology. Disturbed area and forest; ground level to arboreal.

Literature. Hashimoto & Yamane (2014; prey of army ants).

Genus *Prenolepis* Mayr, 1861

Named Bornean species: 3 (Williams & LaPolla 2016). Lambir species: 2 (named).

Prenolepis jerdoni Emery, 1893 (sp. 1 of SKY)

Collection data. 8 ha plot: 6.ii.2020, HOT (CA1086). Lambir’: w, 5.viii.2004, HOT (Ground 04-00121).

Biology. Forest; ground level to arboreal; attracted to extrafloral nectary and cheese baits; active in the daytime.

***Prenolepis subopaca* Emery, 1900 (sp. 2 of SKY)**

Collection data. ‘Lambir’: w, v–vi, HOT & T. Itioka (AT0093); w, 11.ix.2009, Kishimoto & Itioka (CN257); w, 12.ix.2009, same collectors (CN064); w, 24.ix.2010, same collectors (CN053); w, 6.vi.2010, HOT (CA1086); 3–12.ix.2009 (Ant-mimic sample 316).

Taxonomic notes. This species had been treated as a subspecies of the closely related *P. jerdoni* (e.g., Bolton 1995) until Williams & LaPolla (2016) raised it to species status.

Biology. Forest; ground level to canopy. This species is much commoner than *P. jerdoni*. Most of ‘*P. jerdoni*’ mentioned in the following papers can be this species: Tanaka et al. (2012), Hashimoto & Yamane (2014; prey of army ants) and Katayama et al. (2015; supporting information).

Genus *Pseudolasius* Emery, 1887

Named Bornean species: 3 (Pfeiffer et al. 2011). Lambir species: 8 (unidentified). All the forms for which Borneo is the type locality were described from the queen and/or male. All the Lambir species inhabit the forest floor and nest mainly in decayed wood or soil. Foragers generally do not appear on the ground surface.

Unidentified species in *Pseudolasius*: **sp. 3 of SKY** (8 ha plot), **sp. 4 of SKY** (8 ha plot), **sp. 8 of SKY** (50 ha plot, Bt. Lambir), **sp. 9 of SKY** (8 ha plot, 50 ha plot, Sungai Liku: nest in soil <SR04-SKY-15>; ‘Lambir’: nest in soil), **sp. 19 of SKY** (prey of *Aenictus*), **sp. 24 of SKY** (prey of *Aenictus*), sp. 29 of SKY (50 ha plot), **sp. 30 of SKY** (8 ha plot, ‘Lambir’: nest in soil) (**sp. 33 of SKY** (Tourist area: nest under bark of log, SR04-SKY-26)).

Tribe Myrmoteratini Emery, 1895**Genus *Myrmoteras* Forel, 1893**

Named Bornean species: 10 (Pfeiffer et al. 2011). Lambir species: 2 (1 named, 1 unidentified). Two Lambir species belong to the subgenus *Myagroteras* Moffett, 1985.

***Myrmoteras donisthorpei* Wheeler, 1916 (sp. 7 of SKY; = *sp. 14 of SKY*)**

Collection data. Inoue trail: w, 24.iii.2013, SKY (SR04-SKY-36). 50 ha plot: w, 24.iii.2013, SKY. ‘Lambir’: w, 15.viii.1997, SKY; w, 5.xi.2008, M. Yoshima (29-L3/YM-0104).

Biology. Forest; ground level.

Literature. Hashimoto & Yamane (2014; as *M. diastematum*; prey of army ants).

Unidentified species in *Myrmoteras*: **cf. sp. 22 of SKY** (‘Lambir’: C forest floor-9, F83, SQ-1074).

Tribe Oecophyllini Emery, 1895

Genus *Oecophylla* F. Smith, 1860

Named Bornean species: 1 (Pfeiffer et al. 2011). Lambir species: 1 (named).

Oecophylla smaragdina (Fabricius, 1775) (sp. 1 of SKY) (Pl. 8: 36–39)

Collection data. 8 ha plot: w, 6.i.1993, SKY; w, 13.i.1993, honey bait, SKY.

Biology. Forest; arboreal, foragers also seen on ground; nests among woven leaves on trees; carnivorous; attracted to honey and cheese baits. Founding queens have a huge mesosoma and green gaster (Pl. 8: 36, 37).

Literature. Yamane et al. (1996), Hashimoto et al. (1997), Tanaka et al. (2007, 2012), Katayama et al. (2015; supporting information).

Tribe Plagiolepidini Forel, 1886

Genus *Acropyga* Roger, 1862

Named Bornean species: 9 (LaPolla 2004, Pfeiffer et al. 2011). Lambir species: 4 (named). All the Bornean species of this genus live in soil or rotting wood (rarely in epiphytic Araceae on trees) and generally do not appear on the exposed ground surface.

Acropyga acutiventris Roger, 1862 (sp. 1 of SKY)

Collection data. Tourist area: w, 22.i.1993, rotting wood, SKY (2 workers identified by J.S. LaPolla). ‘Lambir’: w, 14.iii.2011, rotting wood, SKY (SR11-SKY-25).

Biology. Forest; ground level; nest in rotting wood.

Acropyga butteli Forel, 1912 (sp. 2 of SKY)

Collection data. 8 ha plot: w, 23.i.1993, SKY; w, 15.viii.1995, 48 m above ground, ex Araceae, T. Yumoto. 50 ha plot: w, 24.iii.2013, ex leaf litter, SKY (SR13-SKY-39).

Biology. Forest; ground level to arboreal.

Literature. LaPolla (2004).

Acropyga inezae Forel, 1912 (sp. 5 of SKY)

Collection data. ‘Lambir’: w, 18.i.2012, Y. Maekawa (LL14-25, 0–10, A8, in soil.

Biology. Forest; ground level; nest in soil.

Literature. Ohashi et al. (2017; as *A. butteli*).

Acropyga nipponensis Terayama, 1985 (sp. 4 of SKY)

Collection data. Inoue trail: w, 29.ix.2005, HOT (AT1108). .

Genus *Anoplolepis* Santschi, 1914

Anoplolepis gracilipes (F. Smith, 1857) (sp. 1 of SKY) (Pl. 7: 34, Pl. 8: 35)

Collection data. 8 ha plot: w, 13.i.1993, honey bait, SKY (G-1-1, 12). HQ: 13–

14.i.1993, SKY. Tourist area: w, 31.xii.1997, F. Yamane.

Biology. Disturbed area and forest; ground level and on tree; attracted to *Endospermum* EFN and honey baits; active during the day and night.

Literature. Yamane et al. (1996).

Genus *Plagiolepis* Mayr, 1861

Named Bornean species: 1 (Pfeiffer et al. 2011). Lambir species: 4 (all unidentified). This genus is mainly distributed in dry areas like Australia, northwest India through Middle Asia to Africa. The *Plagiolepis* fauna of tropical Asia has been almost ignored. The only species so far recorded from Borneo is the tramp *P. alluaudi* Emery, 1894 (Pfeiffer et al. 2011).

Unidentified species in *Plagiolepis*: **sp. 1 of SKY** (8 ha plot), **sp. 2 of SKY** (leaf litter on palm <SR11-SKY-29>), **sp. 3 of SKY** (=sp. 4 of SKY; 8 ha plot, Canopy 4 ha, 'Lambir'; arboreal; nests in compartmentalized space under bark, in aerial soil accumulated at base of epiphyte, and in live liana stem; attracted to cheese baits; active in the daytime; AT0990, AT1013; Tanaka et al. 2012, as sp. 4 of SKY; Katayama et al. 2015, supporting information), and **sp. 6 of SKY** (8 ha plot; ex epiphyte on tree).

Corrigenda and Addenda for Part I: Myrmicinae

P. 194.

Crematogaster ransonneti Mayr, 1868 → *Crematogaster keris* Hosoishi, 2020 [This species belongs to the *C. ransonneti* species group; see Hosoishi 2020, p. 763]

Pp. 201–202.

Myrmecina cf. *bandarensis* Forel, 1913 → *Myrmecina maryatiaae* Okido, Ogata et Hosoishi, 2020 [This is the most common, small species in Borneo; see Okido et al. 2020, p. 72]

Myrmecina sp. 1 of SKY → *Myrmecina spinosa* Okido, Ogata et Hosoishi, 2020

Myrmecina sp. 3 of SKY → *Myrmecina insulana* Okido, Ogata et Hosoishi, 2020 [New to Sarawak. We have a single specimen collected in 8 ha plot on 21.i.1993 by SKY. This species occurs in Borneo, Java, Sumatra and Malay Peninsula.]

Myrmecina sp. 13 of SKY → **Myrmecina andalas* Satria et Yamane, 2019 [New to Borneo. The single specimen from 8 ha plot (14.i.1993, SKY) has slightly larger eyes than the Sumatran specimens (G. Kemiri at 900–1200 m alt.); see Satria & Yamane 2019, p. 185.]

The following species are added to the list.

***Strumigenys leptorhina* Bolton, 2000**

Collection data. ‘Lambir’: w, 28.ix.2013, forest floor, Kitora & Itioka (123/SQ-1129).

Taxonomic notes. This species, described from Sarawak, belongs to the *S. mayri* Emery, 1897-group (Bolton 2000).

***Myrmecina lambirensis* Okido, Ogata et Hosoiishi, 2020**

Collection data. No specimen available.

Taxonomic notes. Okido et al. (2020, p. 59) described this species based on a single worker from Bukit Lambir collected by H. Okido on 22.viii.1995. This species is very unique in having smooth and shiny dorsomedian portion of the mesosoma and lateral portion of the pronotum.

***Paratopula macta* Bolton, 1988 (sp. 1 of SKY)**

Collection data. ‘Lambir’: w, v–vi.2003, HOT & T. Itioka (AT0169).

Biology. Forest; arboreal.

***Paratopula demeta* Bolton, 1988 (sp. 2 of SKY)**

Collection data. ‘Lambir’: w, xii.2003–iii.2004, HOT & T. Itioka (DAT371).

Biology. Forest; arboreal.

Concluding Remarks

A total of 579 ant species belonging to 96 genera in 10 subfamilies have been recorded from Lambir Hills National Park and its close vicinity (Table 1). Our survey covered from the ground level to canopy in primary and secondary forests as well as open/disturbed areas (headquarters and laboratory sector) and forest edge including bushes along the traffic road. Detailed analysis would be made when more sites in Southeast Asia are surveyed for ant fauna, accompanied with reliable species lists.

To date the highest number of ant species recorded from one site in Southeast Asia might be 524 ‘morphospecies’ in a primary rain forest at Poring Hot Spring (ca. 4 km²) covering altitudes from 550 to 800 m (Brühl et al. 1998). They used several techniques for sampling ants from the ground level to canopy. Unfortunately, species list was not presented, though a list is available for the number of species for each of 73 genera collected.

We compare our data with those of two surveys with detailed species lists (Ito et al. 2001, Malsch et al. 2003) for the total species number and the number of species identified to species (Table 2). Ito et al. (2001) studied the diversity of ants in the Bogor Botanical Gardens (Kebun Raya Bogor) situated in the downtown of Bogor, covering an area of ca. 87 ha and with various habitat types. Surprisingly as many as 215 species

Table 1. Comparison of species number among three Southeast Asian sites for which detailed species lists are available.

		Lambir Hills NP		Bogor BG		Pasoh FR	
		Total spp.	Identified spp.	Total spp.	Identified spp.	Total spp.	Identified spp.
Leptanillinae	(total)	1	1	2	2	1	0
	<i>Leptanilla</i>	0	0	2	2	1	0
	<i>Protanilla</i>	1	1	0	0	0	0
Proceratiinae	(total)	9	4	5	2	7	0
	<i>Probolomyrmex</i>	3	3	2	2	2	0
	<i>Discothyrea</i>	3	0	3	0	2	0
	<i>Proceratium</i>	3	1	0	0	3	0
Amblyoponinae	(total)	5	3	4	3	6	2
	<i>Myopopone</i>	1	1	0	0	1	1
	<i>Mystrum</i>	1	1	1	1	1	1
	<i>Prionopelta</i>	1	1	1	1	1	0
	<i>Stigmatomma</i>	2	0	2	1	3	0
Ponerinae	(total)	69	27	43	19	68	23
	<i>Anochetus</i>	8	4	5	2	6	2
	<i>Brachyponera</i>	1	0	2	0	0	0
	<i>Buniapone</i>	1	1	1	1	1	1
	<i>Centromyrmex</i>	2	2	1	1	1	1
	<i>Cryptopone</i>	3	0	2	0	2	0
	<i>Diacamma</i>	2	2	1	1	1	0
	<i>Ectomomyrmex</i>	3	1	1	0	6	1
	<i>Emeryopone</i>	1	1	0	0	2	0
	<i>Euponera</i>	1	1	1	1	1	1
	<i>Harpegnathos</i>	1	1	1	1	1	1
	<i>Hypoponera</i>	15	0	8	0	14	0
	<i>Leptogenys</i>	11	7	6	4	12	6
	<i>Mesoponera</i>	3	0	1	0	1	1
	<i>Myopias</i>	2	0	1	1	1	0
	<i>Odontomachus</i>	1	1	2	2	2	2
	<i>Odontoponera</i>	2	2	2	2	1	1
	<i>Parvaponera</i>	1	1	0	0	1	1
	<i>Platythyrea</i>	3	2	3	2	10	2
	<i>Ponera</i>	7	0	4	0	2	0
	<i>Pseudoneoponera</i>	1	1	1	1	3	3
Dorylinae	(total)	36	24	8	5	27	9
	<i>Aenictus</i>	18	18	3	2	12	7
	<i>Cerapachys</i> (s. lat.)	0	0	0	0	14	1
	<i>Crysapace</i>	1	0	1	1	0	0
	<i>Dorylus</i>	2	2	1	1	1	1
	<i>Lioponera</i>	6	3	0	0	0	0
	<i>Ooceraea</i>	3	0	2	1	0	0
	<i>Parasyscia</i>	3	1	1	0	0	0
	<i>Syscia</i>	3	0	0	0	0	0
Dolichoderinae	(total)	39	26	9	8	29	4
	<i>Chronoxenus</i>	1	0	0	0	0	0
	<i>Dolichoderus</i>	10	8	4	3	3	3
	<i>Iridomyrmex</i>	1	1	0	0	1	0
	<i>Philidris</i>	2	1	0	0	1	0
	<i>Tapinoma</i>	8	2	2	2	9	0
	<i>Technomyrmex</i>	17	14	3	3	15	1
Ectatomminae		11	5	2	2	7	2
	<i>Gnamptogenys</i>	11	5	2	2	7	2

(continued on the next page)

(60% identified) were collected from this small area, including four army ant (*Aenictus*, *Dorylus*) species and even two new species of the rare ant genus *Leptanilla*. This figure may represent the highest number so far recorded from a single arboretum in Asia. A German group (Malsch et al. 2003) listed 489 species (28.6% identified) from Pasoh Forest Reserve that has been the highest species number recorded from one site

(continued from the preceding page)

Formicinae	(total)	177	78	60	26	138	45
<i>Acropyga</i>		4	4	1	1	6	1
<i>Anoplolepis</i>		1	1	1	1	1	1
<i>Camponotus</i>		50	15	9	3	49	9
<i>Cladomyrma</i>		4	3	0	0	1	1
<i>Colobopsis</i>		16	8	4	1	0	0
<i>Dinomyrmex</i>		1	1	0	0	1	1
<i>Euprenolepis</i>		3	2	0	0	2	1
<i>Echinopla</i>		7	3	1	1	6	3
<i>Gesomyrmex</i>		1	1	1	1	1	0
<i>Myrmoteras</i>		2	1	0	0	1	1
<i>Nylanderia</i>		7	0	10 *	0	11 *	0
<i>Oecophylla</i>		1	1	1	1	1	1
<i>Plagiolepis</i>		4	0	0	0	2	0
<i>Paraparatrechina</i>		8	3	0	0	0	0
<i>Paratrechina</i>		1	1	1	1	0	0
<i>Polyrhachis</i>		57	32	25	16	45	25
<i>Prenolepis</i>		2	2	0	0	2	1
<i>Pseudolasius</i>		8	0	6	0	9	0
Myrmicinae	(total)	219	129	78	50	199	52
<i>Aphaenogaster</i>		1	0	0	0	0	0
<i>Epelysidris</i>		1	0	1	1	0	0
<i>Myrmecaria</i>		9	6	1	1	2	0
<i>Monomorium</i>		9	2	4	2	10	1
<i>Solenopsis</i>		1	0	1	0	5	0
<i>Sylophopsis</i>		1	1	1	1	1	0
<i>Trichomyrmex</i>		0	0	1	1	0	0
<i>Pheidole</i>		22	20	14	10	39	5
<i>Eurhopalothrix</i>		0	0	1	0	1	1
<i>Strumigenys (Pyramica)</i>		2	1	2	2	5	1
<i>Strumigenys (s. str.)</i>		22	18	8	3	18	6
<i>Acanthomyrmex</i>		2	2	0	0	2	1
<i>Calyptomyrmex</i>		5	3	1	0	0	0
<i>Cardiocondyla</i>		8	1	5	3	4	0
<i>Carebara (Carebara)</i>		0	0	0	0	1	0
<i>Carebara (Oligomyrmex)</i>		7	0	5	0	14	0
<i>Carebara (Pheidologeton)</i>		3	2	1	1	3	2
<i>Cataulacus</i>		6	5	1	1	5	4
<i>Crematogaster</i>		46	30	6	5	30	3
<i>Dacotinops</i>		2	2	0	0	0	0
<i>Dilobocondyla</i>		3	1	0	0	2	1
<i>Gauromyrmex</i>		2	0	0	0	0	0
<i>Lophomyrmex</i>		1	1	1	1	1	1
<i>Lordomyrma</i>		2	0	1	0	1	0
<i>Mayriella</i>		1	1	0	0	1	0
<i>Meranoplus</i>		2	2	2	2	4	3
<i>Myrmecina</i>		5	5	3	3	7	0
<i>Paratopula</i>		2	2	0	0	1	1
<i>Pristomyrmex</i>		4	3	1	1	5	1
<i>Proatta</i>		1	1	0	0	1	1
<i>Recurvidris</i>		3	2	1	1	2	2
<i>Rhopalomastix</i>		1	0	1	0	1	1
<i>Rostromyrmex</i>		0	0	0	0	1	1
<i>Tetheamyrmex</i>		0	0	0	0	1	1
<i>Tetramorium</i>		30	14	11	10	20	13
<i>Vollenhovia</i>		14	4	4	1	11 **	2
<i>Vomvisidris</i>		1	0	0	0	0	0
Pseudomyrmecinae	(total)	13	12	4	2	7	3
<i>Tetraponera</i>		13	12	4	2	7	3

* Including species of *Paraparatrechina*.

** Probably including species of *Gauromyrmex*.

composed of natural and seminatural forests in Southeast Asia on the basis of reliable species sorting. In all of these data including ours the pattern of dominant subfamilies is similar to each other; the myrmecine ants occupied the first rank (36.3–40.7% of the total species), followed by Formicinae (27.9–30.0) and Ponerinae (11.9–20.0). The highest proportion for the Ponerinae observed in Bogor (20.0%) might be due to the

extraordinary effort by F. Ito looking for nests in soil and on ground surface.

The total species number in Lambir (579) exceeds the former records with high species numbers, i.e., Poring Hot Spring (524) and Pasoh (489). Most of our effort at the ground level was made during the early half of 1990s when our skill to collect ants was very primitive. We only used mesh-type sifters, pans and scoops; Winkler sifters have never been used to sample leaf litter ants. This may be one reason for the very poor species number (2) in '*Pyramica*', for which 21 species have been known from Borneo (Bolton 2000, Pfeiffer et al. 2011). Pitfall traps were also not used that are known to be very effective particularly during the night. However, our frequent patrol along forest trails during both the daytime and nighttime has produced the highest species number (18) for the army ant genus *Aenictus* in Asia. Arboreal and canopy species were rather efficiently sampled with the canopy walk-way system, canopy crane and direct climbing onto tall trees (see Part I).

Table 2. Number of species in each subfamily in three Southeast Asian sites with detailed species lists.

	Lambir Hills NP		Bogor BG		Pasoh FR	
	Total spp.	Identified spp.	Total spp.	Identified spp.	Total spp.	Identified spp.
Leptanillinae	1	1	2	2	1	0
Proceratiinae	9	4	5	2	7	0
Amblyoponinae	5	3	4	3	6	2
Ponerinae	69	27	43	19	68	23
Dorylinae	36	24	8	5	27	9
Dolichoderinae	39	26	9	8	29	4
Ectatomminae	11	5	2	2	7	2
Formicinae	177	78	60	36	138	45
Myrmicinae	219	129	78	50	199	52
Pseudomyrmecinae	13	12	4	2	7	3
(total)	579	309	215	129	489	140

Biological information on Lambir ants was obtained through general collecting, ecological surveys on ant-plant relationship and on species interaction in the canopy, etc. During the early half of 1990s we were mainly interested in foraging workers at the ground level, thus often ignored their nests and failed to record their relationships with other insects and plants. On the other hand, at around 2000 we started to sample ants from nests on trees and in canopies, this having brought about rich information on their biology. We have confirmed nest sites only for 154 species (26.7% of the total species), while 199 species (40.7%) were confirmed for their nesting sites in Pasoh (Malsch et al. 2003). Hashimoto et al. (2006) reported nest sites of 57 species (27.8%) of the total 205 species in a rain forest in Danum Valley Conservation Area, Sabah. We have much more

information on the nesting site of ants obtained recently in various parts of Southeast Asia. Combining all these data, we will get a more accurate picture about nesting site for the species in each genus and forest stratum.

Plant-ant relationships were extensively studied in Pasoh with a special reference to extrafloral nectaries (Fiala & Guan 2003). They listed slightly less than 30 ant species attracted to extrafloral nectaries, nine species being in *Polyrhachis*. In Lambir 27 species were observed at extrafloral nectaries, of which 21 belonged to Formicinae (mainly *Camponotus*, *Colobopsis* and *Polyrhachis*). Thirteen species were observed attending hemipterans, mostly scales and aphids (Homoptera) but including one species of bug (Heteroptera), to take honeydew. Many more species, 68, were sampled with honey or sugar baits. Among the 579 species recorded from Lambir 88 species (15.2%) were attracted to extrafloral nectaries, hemipteran honeydew or honey/sugar baits. The number will rise with increasing intensive surveys focusing on these sugar sources.

Finally, we like to emphasize the importance of taxonomic study on Asian ants. We can compare biological data of ants among various sites/localities only if most of the species have their scientific names. In our study in Lambir only 53.5% were identified to species, other species being reported with species-codes. For a further clarification at species level, ant taxonomists in different countries need cooperate each other; the most important would be quick and easy cross-checking of specimens between countries that is, however, becoming more and more difficult due to the strict control for biological specimens. We hope some young taxonomists will tackle revisions of difficult groups like *Vollenhovia*, *Carebara* ('*Oligomyrmex*'), *Camponotus* (*Tanaemyrmex*), *Nylanderia* and groups that wait descriptions of many new species.

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*: papers dealing with Lambir ants other than Myrmicinae and Pseudomyrmecinae.

Explanation of figures

- Plate 1.** 1: Foragers of *Leptogenys diminuta* (Photo: SKY, May 2011). 2: Foragers of *L. processionalis distinguenda* (Photo: SKY, 14 May 2011). 3: *Pseudoneoponera tridentata* worker on forest floor (Photo: SKY, 3 August 1995). 4: *P. tridentata* worker releasing foam from the tip of the gaster (*ditto*). 5: *Diacamma intricatum* worker picking up an adult moth (Photo: SKY, March 2013). 6: *D. intricatum* workers transporting a queen of *Oecophylla smaragdina* that was still alive (Photo: SKY, August 1995).
- Plate 2.** 7: *Odontoponera denticulata* worker on the ground (Photo: SKY, 13 August 1995). 8: *O. denticulata* foragers attracted to powdered-cheese bait (Photo: SKY, 14 May 2011). 9: *Aenictus laeviceps* foragers climbing a tree trunk in the night (Photo: SKY, 14 May 2011). 10: *A. laeviceps* foragers carrying a formicine ant in group (Photo: SKY, 1 January 1998). 11: *Dorylus vishnui* workers coming out onto ground surface (Photographer unknown, January 1993).
- Plate 3.** 12: Nest of *Dolichoderus cuspidatus* made in a big tree hollow (Photo: SKY, 6 August 1995). 13: Same nest. Workers handling a mosquito presented by us. They were puzzled with the 'prey', which was finally discarded. 14: *Dolichoderus thoracicus* workers gathering with their symbiont mealybugs on a legume fruit (Fabaceae) in the forest canopy (Photo: TI, 3 December 2012).
- Plate 4.** 15: *Dolichoderus thoracicus* workers on a satellite nest with cover leaf removed. Naked pupae are seen among them (Photo: Iku A, 1 March 2018). 16: Nest of *D. thoracicus* among woven leaves. Possibly they used an abandoned nest of spider (Photo: SKY, 22 March 2013). 17: Workers of *Technomyrmex* sp. (*T. albipes* species group) attending hemipteran larvae and adults on a bamboo shoot (Photo: TI, 30 November 2015). 18: *Camponotus (Myrmoplatys)* sp. 21 of SKY living on *Korthalsia* (rattan) stem. Workers are very aggressive (Photo: SKY, 13 May 2011). 19: *Camponotus (Myrmotarsus) irritabilis* workers observed in the night (Photo: SKY, 16 August 1995). 20: Lycaenid mature larva just having appeared from a nest of *Camponotus (Myrmotarsus) rufifemur* in tree hollow in the night (Photo: SKY, 5 August 1995).
- Plate 5.** 21: Trail sharing by *Camponotus (Myrmotarsus)* sp. and *Crematogaster* ('*Physocrema*') sp. (Photo: SKY, 12 August, 1995). 22: Workers of *Colobopsis* cf. *saundersi* handling a dipteran presented to them by us (Photo: SKY, 20 August 1995). 23: *Camponotus (Tanaemyrmex)* sp. worker receiving a drop of honeydew from a bug (Photo: SKY, 25 August 1995). 24: Honey-bait occupied by *Camponotus*

(*Tanaemyrmex*) sp. 15 of SKY. This species has color dimorphism in the worker caste; major workers have orange heads (Photo: SKY, 13 January 1993). **25:** *Dinomyrmex gigas* major worker, with a huge head (Photo: SKY, 19 September 1998). **26:** *D. gigas* worker corpse parasitized with a fungus (Photo: SKY, 23 March 2013).

Plate 6. **27:** Minor workers of *Dinomyrmex gigas* collecting muscle of a dead beetle (Photo: SKY, March 2013). **28:** *D. gigas* attacking a freshly killed reptile (Photo: SKY, date unknown).

Plate 7. **29:** Nest of *Polyrhachis (Myrmhopla) abdominalis* under the bark of a live tree, with a worker, larvae and cocoons (Photo: SKY, date unknown). **30:** *P. (Polyrhachis) bihamata* workers attracted to powdered-cheese bait (Photo: SKY, 18 August 1995). **31:** Nest (95-L-02) of *P. (Myrmhopla)* sp. 4 of SKY in a rolled leaf (Photo: SKY, 4 August 1995). **32:** Ant mimicking spider, *Corinnomma* sp. (Araneae: Corinnidae), found on a *Polyrhachis bihamata* trail near the nest (Photo: SKY, August 1995). **33:** *Polyrhachis (Myrmhopla) armata* on a leaf. Two winged ants are males (Photo: Iku A, 8 December 2017). **34:** *Anoplolepis gracilipes* workers attending a larva of *Allotinus unicolor* (Lycaenidae, Lepidoptera) feeding on aphids (Photo: TI, 16 October 2012).

Plate 8. **35:** *Anoplolepis gracilipes* workers attending scale insects (Photo: TI, 19 January 2007). **36 & 37:** Founding queen of *Oecophylla smaragdina* (Photo: Iku A, 4 June 2018). **38:** *O. smaragdina* foragers transporting a large curculionid beetle (Photo: SKY, 21 March 2013). **39:** *O. smaragdina* foragers carrying a reptile corpse on house wall heading for their arboreal nest (Photo: SKY, 23 March 2013).



Plate 1

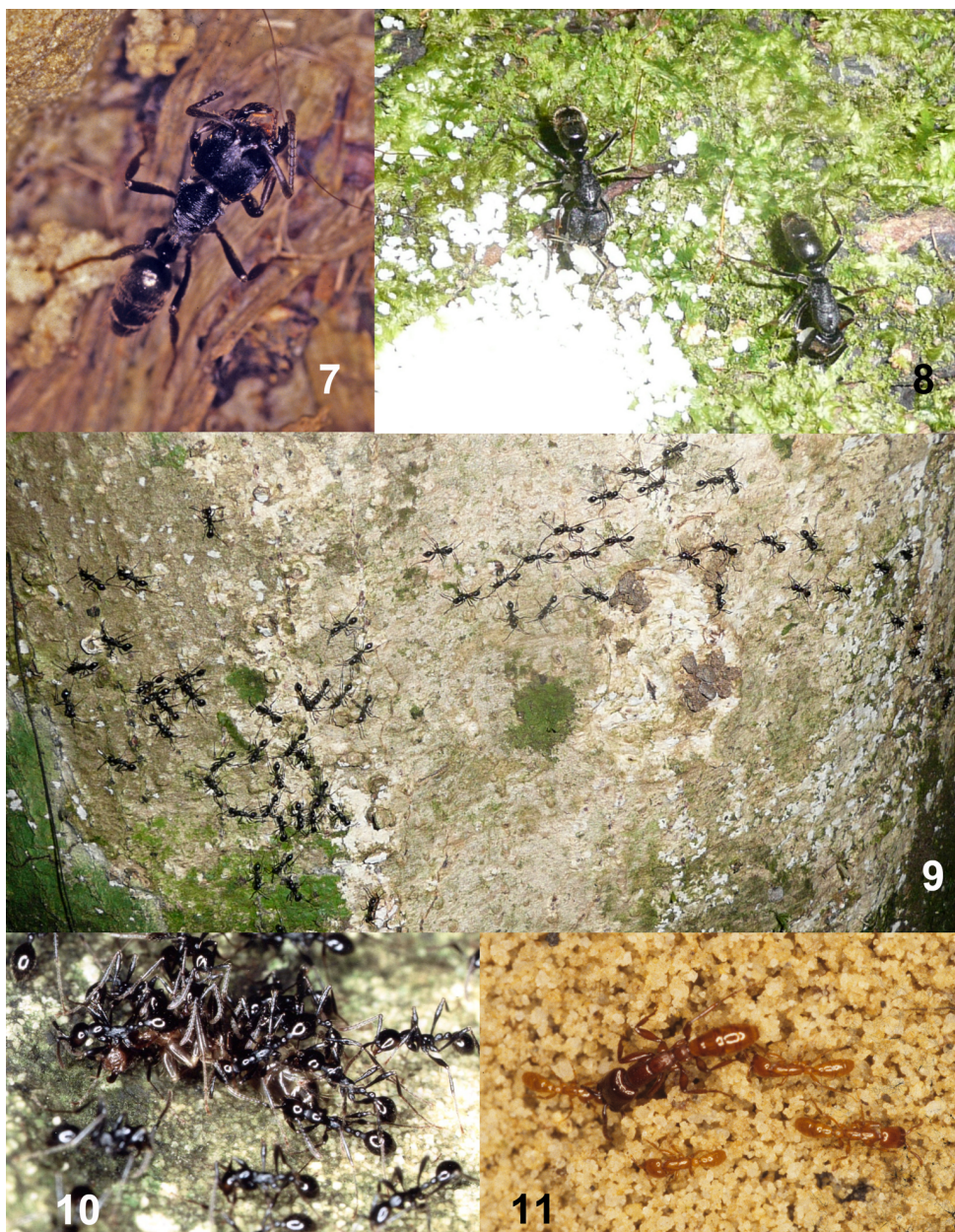
**Plate 2**



Plate 3

**Plate 4**



Plate 5



Plate 6



Plate 7

**Plate 8**

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