The Formicidae of Borneo (Insecta: Hymenoptera):
a preliminary species list

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ABSTRACT. More than ninety years after Wheeler’s 1919 “Ants of Borneo,” we present a comprehensive list of the Bornean ant fauna, recorded in the states of Brunei, Sabah and Sarawak (Malaysia), and Kalimantan (Indonesia). Our critical review of ant literature resulted in a catalogue of 97 ant genera with 717 valid species and 52 additional subspecies of ants from 12 subfamilies, including eight genera for which, up to now, only morphospecies have been recorded in Borneo. The subfamilies Myrmicinae (315) and Formicinae (213) comprised the most species; the most speciose genera were Polyrhachis (98) and Strumigenys (71), followed by Pheidole, Camponotus and Crematogaster. However, half of the Bornean ant genera included only one or two species, for example, the endemic monotypic genera Anomalomyrma, Bregmatomyrma, Ishakidris, Loweriella, Secostruma and Tetheamyrma. Ant taxonomic research in Borneo dates back to the nineteen century and has resulted in 418 type descriptions, of which 390 are currently valid. Since many habitats of Borneo have still not been effectively sampled, the actual number of Bornean ant species may be much higher; we estimate that at least 1,100 species are to be expected. As destruction of natural habitat on Borneo is accelerating, great conservation efforts must urgently be made if current ant diversity is to be saved.

Keywords: ants, biodiversity, conservation, checklist, endemism, faunistic similarity, Indonesia, Malaysia, species classification, taxonomic history

INTRODUCTION

Species checklists have for a long time been regarded by some as an outdated scientific contribution, and still seem to be considered as of minor value for the scientific community, given the low impact factor these publications usually achieve (Ware 1990, Krell 2000). However, they can be essential instruments for species conservation and of high value to conservation policy. Given today’s dramatic pressures on biodiversity and the ongoing
destruction and conversion of natural landscapes worldwide, species checklists are fundamental to conservation, as sound knowledge of the present state of the biota is a basis for all future conservation actions.

Tropical Southeast Asia comprises four of the 25 biodiversity hotspots defined by Myers et al. (2000). One of these hotspots is the Sundaland subregion, which covers the areas of the Malay Peninsula, Sumatra, Java and Borneo. This region is very rich, both in species numbers and endemism, but its biodiversity is particularly endangered by habitat loss, fragmentation and degradation that are operating on a massive scale (Sodhi et al. 2004). In particular Borneo, the world’s third-largest island, is experiencing one of the highest rates of habitat destruction. The current deforestation rate for Borneo has been calculated on a long-term basis to be about 8,800 km$^2$ per year (Stibig & Malingreau 2003). Based on this rate the island has lost over 30 percent of its forest cover in the last twenty years and just one-third of Borneo will remain forested by 2020 (Rautner et al. 2005, Stibig et al. 2007). Thus, within half a human generation, much of the biodiversity in the splendid lowland primary forests of Borneo will be lost, probably including many species unknown to science.

Our species list aims at recording the present state of knowledge of the Bornean fauna of ants, a family of insects with special significance for ecology and ecosystem functioning. Ants are virtually everywhere, especially in the tropics, where they exhibit an amazing diversity, populating all forest strata, acting as mutualists, predators, prey and bioturbators (Folgarait 1998). Recent ant studies in Malaysian Borneo have found 61 species on a single rainforest tree in Sabah (Floren & Linsenmair 1997), 32 species in a single square metre of forest floor, 206 species in soil and leaf litter on 100 m² of Gunung Mulu National Park in Sarawak (Mezger & Pfeiffer, forthcoming) and 640 species sampled over a series of studies in Poring Hot Springs, Kinabalu National Park in all strata of a tropical rainforest (Brühl et al. 1998, Pfeiffer 2005).

Ant research on Borneo started long ago with the work of Le Guillou in 1842, who described Diacamma rugosum and Polyrhachis arcuata from the island. In 1841, the English adventurer James Brook had been proclaimed Rajah of Sarawak and he turned out to be a patron and frequent host for nineteen century naturalists. The famous A.R. Wallace was his guest during 1855, and ten years later he invited the botanist O. Beccari to Kuching. Both men were diligent collectors of ants and their collections were evaluated by the most important ant taxonomists of the time. In 1857, F. Smith published “Catalogue of the hymenopterous insects collected at Sarawak, Borneo; Mount Ophir, Malacca; and at Singapore, by A. R. Wallace,” which contained the first species list of Bornean ants; and in 1872, G. Mayr wrote “Formicidae Borneenses collectae a J. Doria et O. Beccari in territorio Sarawak annis 1865–1867.” Both papers were for a long time the best sources of information about the ant fauna of the island. A much more comprehensive species list was published in 1919, when W.M. Wheeler released his famous “Ants of Borneo,” which included records and descriptions of more than 260 species. This paper was until now the most important directory of Bornean ants, as the 1951 “Checklist of the ants of Asia” (Chapman & Chapco 1951) cited only some of its species and included no further information for Borneo. Later studies focused on the description of certain systematic groups, rather than on documentation of overall faunal diversity, but recent research on Bornean ants resulted in ample taxonomic inventories (e.g., Bolton 2000, 2007; Eguchi 2001).

In spite of all efforts at species identification and due to the extremely high biodiversity, many recent ecological studies on Bornean ants are still working with a high proportion of morphospecies, rather than using exact species classifications, and it is therefore difficult to assess total species richness or beta diversity of plots within the region. However, for more than ten years, web-based databases (e.g., antbase.org, AntWeb, AntBase.Net) have been available that provide help in the identification of ant specimens, by supplying a variety of tools including specimen photographs, keys, and location records. The species list we present here may further help researchers investigate the Formicidae of Borneo, as it includes all recorded species. Thus, it provides a platform for further myrmecological research on the island. Hopefully, it will also help to conserve this most interesting
fauna, to which ant researchers have dedicated many of their studies.

**MATERIALS AND METHODS**

We collected all available information about ant species from Borneo, including revisions of species groups, original species descriptions, and species lists from the Internet. We used the Primary Taxonomic Publications Databank on www.antbase.org (Agosti & Johnson 2005) to assess the available taxonomic literature. Additionally, we searched for species records and photographs of ant species from Borneo in the online databases www.antweb.org (Fisher 2002–2011) and www.antbase.net (Pfeiffer 2003–2011) and included those species in our list for which specimen records were available. Moreover, 116 specimen records from Borneo were collected during a stay in the Natural History Museum London (BMNH) and 150 records came from the AntBase.Net Collection of the University of Ulm (ABNC), which is curated by the first author. Additional collection records were included from Rudy Kohout and Bakhtiar Effendi Yahya. All data were cross-checked to assess their validity and the correctness of species identifications. All species names were first checked by the Hymenoptera name server at www.antbase.org (Agosti & Johnson 2005) to assess synonyms and relevant species descriptions and were later confirmed based on the work of Bolton (1995, 2007, 2010), especially his world species list on www.antweb.org (Bolton 2010). On subfamily and genus level, we entirely followed Bolton’s nomenclature (e.g., Bolton 1999, 2000), not diverging opinions (e.g., Baroni Urbani & De Andrade 2007). Some open questions were resolved by direct communication with other taxonomists (B. Bolton, B. Seifert, M.G. Branstetter, M.L. Borowiec). While most species records were assessed from the literature, we included new records for certain species and genera from the collections of the authors. Only extant species were considered (for the record of a fossil species, see De Andrade & Baroni Urbani 2004) and nominate subspecies are not listed. We compared the Bornean species list with lists recently presented for the Philippines (Alpert & General 2010) and New Guinea (Janda 2010) and assessed the similarity of the species pools using the Sörensen Index. To compare regional ant faunas, we used the software SPADE (Chao & Shen 2009) to calculate the incidence-based Sörensen Index, following the formula

\[ SD = 2D_{1,2}/(D_1 + D_2), \]

with \( D_1 \) and \( D_2 \) being the species richness of each of two communities, and \( D_{1,2} \) being the number of species they share. We used Venn diagrams to distinguish the different subsets of those species.

**RESULTS**

**Literature survey**

The ant fauna of Borneo Island is highly diverse and unique. Our preliminary list of the Bornean ant species comprises 717 species and 52 additional subspecies of ants for which valid names were accessible (see Appendix 1). These species originate from 89 genera; additionally, we found eight genera for which only morphospecies have been listed until now. The Bornean ant fauna comprises 12 subfamilies of ants, with very varied contributions to overall species richness (Table 1). The largest number of described species (315) is in the Myrmicinae, but Formicinae is also strongly represented (213 species). These two subfamilies comprise more than 70 percent of the valid Bornean ant species and subspecies, while the smallest five subfamilies together have less than 5 percent.

The most speciose and commonly encountered genera are *Polyrhachis* (98 species), *Strumigenys* (71 species), *Pheidole* (56 species), *Camponotus* (55 species) and *Crematogaster* (33 species) (see Table 2). Other genera with many species in Borneo include *Cerapachys*, *Dolichoderus*, *Europhalothrix*, *Gnamptogenys*, *Myrmicaria* and *Myrmoteras* (for number of species, see Table 2). However, these figures are skewed by the presence of recent species-rank revisions for many of them. There are other genera with large numbers of Bornean species, but as most of these remain unnamed, they do not show up in this paper. For example, *Hypoponera*, *Myrmecina*, *Tapinoma*, *Nylanderia*, and *Carebara* all have many undescribed Bornean species, as indicated by museum collections (B. Bolton, pers. comm.). Characteristically, for Borneo there are also many monotypic genera,
Table 1: Diversity of Bornean subfamilies of ants. Given for each subfamily is the respective number of genera, species and non-nominate subspecies, the total number of taxa (species and non-nominate subspecies), and the proportion of all ant taxa they contribute.

<table>
<thead>
<tr>
<th>Subfamily</th>
<th>Genera</th>
<th>Species</th>
<th>Subspecies</th>
<th>Species + subspecies</th>
<th>Percentage of taxa</th>
</tr>
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<tbody>
<tr>
<td>Myrmicinae</td>
<td>42</td>
<td>315</td>
<td>17</td>
<td>332</td>
<td>43.2</td>
</tr>
<tr>
<td>Formicinae</td>
<td>19</td>
<td>213</td>
<td>21</td>
<td>234</td>
<td>30.4</td>
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<tr>
<td>Ponerinae</td>
<td>14</td>
<td>59</td>
<td>10</td>
<td>69</td>
<td>9.0</td>
</tr>
<tr>
<td>Dolichoderinae</td>
<td>6</td>
<td>49</td>
<td>4</td>
<td>53</td>
<td>6.9</td>
</tr>
<tr>
<td>Ectatommatinae</td>
<td>2</td>
<td>22</td>
<td>0</td>
<td>22</td>
<td>2.9</td>
</tr>
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<td>1</td>
<td>14</td>
<td>0</td>
<td>14</td>
<td>1.8</td>
</tr>
<tr>
<td>Proceratiinae</td>
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<td>12</td>
<td>0</td>
<td>12</td>
<td>1.6</td>
</tr>
<tr>
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<td>0</td>
<td>10</td>
<td>1.3</td>
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<td>Amblyoponinae</td>
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<td>0</td>
<td>3</td>
<td>0.4</td>
</tr>
<tr>
<td>Leptanillinae</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>0.3</td>
</tr>
<tr>
<td>Dorylinae</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>0.3</td>
</tr>
<tr>
<td><strong>All</strong></td>
<td><strong>97</strong></td>
<td><strong>717</strong></td>
<td><strong>52</strong></td>
<td><strong>769</strong></td>
<td><strong>100</strong></td>
</tr>
</tbody>
</table>

*Fig. 1.* Species richness of Bornean ant genera. The skewed distribution, featuring many genera with only a few species, is characteristic of tropical species assemblages. Subspecies, and genera without valid species, were excluded.
like the ecologically dominant *Oecophylla*, or the endemic *Anomalomyrma*¹, *Bregmatomyrma, Ishakidris, Loweriella, Propodilobus, Secostruma* and *Tetheamyrma*. Indeed, if Bornean ant genera are sorted by their species richness, the resulting curve is highly skewed (Fig. 1); while a few ant genera are speciose, the vast majority comprise much fewer species and subspecies. For the 89 genera for which valid species have been assigned, the species-genera ratio is only 8.06 (S.D. = 15.4), while the median number of species per genus is only 2.0.

Of the 769 listed taxa, 389 were originally described from Borneo; this rises to 417 if we include descriptions of synonyms, and the localities of paratypes. This high proportion points to both the diverse ant fauna of Borneo and the long history of taxonomic research on the island. In 2000, Bolton’s revision of the Dacetini, with 64 new species described from Borneo, provided a sharp extension of the list (Fig. 2).

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¹*Anomalomyrma* is officially a monotypic genus. A second name, *A. kubotai* has been used in Japan but this name is currently unavailable.

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*Fig. 2.* History of taxonomic inventory of the Bornean ant fauna. Given are the yearly (left Y-axis) and cumulative (right Y-axis) numbers of all valid ant species and subspecies described from Borneo in the years 1760 to 2009. Note the different scaling of the left and right Y-Axes. In 1857, F. Smith recorded 37 new species from Borneo, bringing the number of valid ant taxa described from the island to 40, and the number recorded to 88. In 2000, Bolton and Eguchi altogether described 67 new species of ants, bringing the cumulative totals to 307 described and 652 recorded.
Table 2: Number of valid Bornean ant species (excluding subspecies) per ant genus

<table>
<thead>
<tr>
<th>Genus</th>
<th>No. of species</th>
<th>Genus</th>
<th>No. of species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Polyrhachis</td>
<td>98</td>
<td>Paraparatrechina</td>
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<tr>
<td>Strumigenys</td>
<td>71</td>
<td>Philidris</td>
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<tr>
<td>Pheidole</td>
<td>56</td>
<td>Platthyrea</td>
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</tr>
<tr>
<td>Camponotus</td>
<td>55</td>
<td>Probolomyrmex</td>
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</tr>
<tr>
<td>Crematogaster</td>
<td>33</td>
<td>Recurvidris</td>
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<td>Technomyrmex</td>
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</tr>
<tr>
<td>Tetramorium</td>
<td>26</td>
<td>Anomalomyrma</td>
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</tr>
<tr>
<td>Gnamptogenys</td>
<td>22</td>
<td>Anoplolepis</td>
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<tr>
<td>Pyramica</td>
<td>21</td>
<td>Bregmatomyrma</td>
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</tr>
<tr>
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<td>Calyptomyrmex</td>
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<tr>
<td>Dolichoderus</td>
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<td>Chimaeridris</td>
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<tr>
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<td>Lepisiota</td>
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</tr>
<tr>
<td>Acropyga</td>
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<td>Lordomyrma</td>
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</tr>
<tr>
<td>Anochetus</td>
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<td>Loweriella</td>
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</tr>
<tr>
<td>Eurhopalothrix</td>
<td>9</td>
<td>Mayriella</td>
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<tr>
<td>Vollenhovia</td>
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<td>Monomorium</td>
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<td>Myrmirium</td>
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<td>Meranoplus</td>
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<td>Prionopelta</td>
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<td>Proatta</td>
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<td>Diacamma</td>
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Table 2 (continued)

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<thead>
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<th>No. of species</th>
<th>Genus</th>
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<td><em>Odontoponera</em></td>
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</tr>
</tbody>
</table>

**Records for new Bornean ant species**

Our species list (Appendix 1) comprises several species newly recorded for Borneo. These are:

**Polyrhachis (Polyrhachis) craddocki Bingham, 1903**

**Polyrhachis (Myrmhopla) ochracea Karavaiev, 1927**

**Polyrhachis (Myrmothrinax) frauenfeldi subsp. sanguinea Forel, 1911**

**Polyrhachis (Myrmhopla) sumatrensis F. Smith, 1858**

**Polyrhachis (Myrmhopla) tubifex Karavaiev, 1926**
**Myrmicaria arachnoides adpressipilosa Santschi, 1928**

**Myrmicaria birmana Forel, 1902**

**Strumigenys rogeri Emery, 1890**

**Regional beta diversity patterns**
For Borneo (B), we found 97 genera of ants with 717 species, while 84 genera (715 species) are reported for New Guinea (NG) (Janda 2010) and 82 genera (400 species) for the Philippines (P) (Alpert & General 2010). When we compared the ant faunas using the Sörensen Index, which ranges from 0 (zero similarity) to 1 (equality), we found relatively high index values for ant genera (B–NG: 0.71, B–P: 0.80, NG–P: 0.81), while similarity was much lower at species level (B–NG: 0.11, B–P: 0.32, NG–P: 0.16). The corresponding raw data are given in Fig. 3. However, results have to be treated as preliminary, as all data sets are incomplete. For Sundaland, no corresponding data were available.

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**Fig. 3.** Venn diagrams illustrating the overlap of ant genera (left) and ant species (right) between Borneo, New Guinea, and the Philippines. The total number of ant genera is 121, with 97 genera (717 species) from Borneo, 84 genera (715 species) from New Guinea, and 82 genera (400 species) from the Philippines. The total number of ant species is 1,542; subspecies were ignored. Venn diagrams demonstrate the species subsets of the respective areas: e.g., Fig. 3a shows 61 genera found in all three areas, three shared only by Borneo and New Guinea (so altogether 64 genera in common), and 11 only with the Philippines (altogether 72 in common), while 22 genera are restricted to Borneo island.
DISCUSSION

Borneo’s ant fauna includes 12 subfamilies, with at least 97 genera and 769 species and subspecies. Worldwide, there are 22 subfamilies, 299 genera and 14,095 described species of ants (Bolton 2010). Thus, Borneo has representatives of about a third of the world’s genera and about 5.5 percent of its species, though Borneo represents only about 0.5 percent of the earth’s land surface. For comparison, temperate Mongolia, twice the size, harbours about 6 percent of world genera and 0.5 percent of species (Pfeiffer et al. 2007).

Our species list comprises records from more than two hundred years of ant research. It is clear that not all data are equally reliable, but it would be inappropriate to exclude older data, especially since all the material (species descriptions, etc.) is now well documented and easily accessible via the Internet (Agosti & Johnson 2005). The taxonomic literature is subject to frequent revisions and so we were able to find redundant citations for most of the species. The quality of each record can be accessed by evaluating the respective references. However, we have excluded the most doubtful records and commented on others. For example, Polyrhachis relucens and Myrmicaria brunnea were both listed for Borneo by Wheeler (1919), but recent results show that P. relucens is endemic to New Guinea (R. Kohout, pers. comm.), while M. brunnea is confined to the mainland of Asia (Bakhtiar E.Y., pers. comm.). These and other errors (e.g., from Chapman & Capco 1951) were deleted from the list without comment since the purpose of the present paper is to list the species reliably recorded from Borneo. Species suspected to occur but not listed here should be verified through field collection or study of unidentified specimens.

Species that have been recorded on the small island of Pulau Laut, about 400 km northeast of Kuching, for example, Lepisiota rothneyi sundaica, have traditionally been included with the Bornean records, and we follow the same convention. Wheeler (1919, p. 65) reported “Myrmica ritaie” from “Pulo Laut” collected by W. Doherty; however, the type specimen of Myrmica ritaie was found at Mt. Moolegit in Myanmar and the record of a Myrmica species from a location so far south had seemed dubious. Nonetheless, recent research by Radchenko & Elmes (2009) revealed that in Emery’s material collected on Pulau Laut and housed in the Museum of Natural History in Genoa was indeed a new—the southernmost—Myrmica species, which was named “Myrmica emeryi” and is included in the Borneo list. Similarly, Polyrhachis craddocki, reported above for the first time from Borneo, was previously known only from Myanmar (Bingham 1903).

Some species which have to date been recorded only from regions adjacent to Borneo might occur on Borneo itself, but they are omitted from the list because their presence has not been confirmed. For example, the almost-cosmopolitan tramp species Monomorium destructor (Jerdon, 1851) is recorded from the Malay Peninsula, Java, the Philippines and Sulawesi (Wetterer 2009), but not from Borneo itself; however, it is likely that this distribution gap represents only a sampling artefact. Similarly, Amblyopone reclinata is distributed from Java to the Philippines, but is not listed for Borneo, while Overbeckia subclavata and Tyramonymex sp. are registered for Malaysia and the Philippines, but have not yet been recorded in Borneo (www.antweb.org).

The ant species richness of the island has still not been assessed. The current number of 717 described species may comprise only about one-half to two-thirds of the expected total, but available data do not allow meaningful estimate of the actual figure. Although many of the large and striking species may have already been named, especially those from the lower strata, little is known about some of the ecologically-cryptic ant genera, for example, Pseudolasius, Myrmecina, Carebara and Hypoponera. Even in some more conspicuous ant genera few species are described, for example, in Paraparatatrechina and Philidris. Similarly, we expect additional species even for Camponotus, although our list already comprises 70 species and subspecies. In Crematogaster, we currently recognise about 11 additional undescribed species (Hosoishi, own observations), in Polyrhachis, 48 new species are presently under description (Kohout, manuscript in preparation) and for Myrmicaria, six new species from Borneo will be described soon (Bakhtiar, manuscript in preparation). Tetramorium is another genus with many species
awaiting formal description; the BMNH alone holds specimens of about 100 undescribed *Tetramorium* from the Indo-Australian region, including many from Borneo (B. Bolton, pers. comm.; see also Sorger 2011, this issue of AM).

Numerous habitats of Borneo remain to be sampled in detail; these include mangroves, kerangas, swamp forest, and the various mountains of the island, especially limestone mountains. The latter proved to be the most species-rich habitat in our study in Gunung Mulu National Park (Mezger & Pfeiffer, 2011a). In fact, most Bornean ant research has concentrated on only a few locations: Gunung Mulu National Park, Gunung Kinabalu National Park, Danum Valley and Lambir Hills Park have been well sampled in modern times, while Tadjong (Tanjong near Sri Aman, Sarawak) and Hayvep were favourite sites of former ant collectors. More species doubtless await discovery at other places, especially since most of Kalimantan is not sampled at all. Although the highly diverse lowland sites have been almost cleared, high ant diversity may be predicted in the vast mountain ranges of Borneo, as ecological theory predicts the highest species richness is in the middle of an island (Colwell & Lees 2000). In this area, the chances for a diversification of the ant fauna are quite high, for example, when differing geological or altitudinal patterns provide more patchy habitat structure that leads to isolation of subpopulations. Recent studies have shown that a large proportion of soil and leaf litter ant species have indicator value for the forest types in which they have been collected (Mezger & Pfeiffer, 2011b, this issue of AM), so abiotic factors have considerable impact on ant diversity. Due to the high habitat heterogeneity, species diversity in Bornean mountains is driven by high beta diversity between habitats, rather than by high values of alpha diversity at single locations (Mezger & Pfeiffer, forthcoming).

Faunal surveys should include exhaustive methods (like Winkler sampling and insecticide fogging) as well as nest sampling, as each method has different merits.

A certain proportion of the Bornean ant species seem to be restricted to the topsoil (the first 5 to 15 cm of soil with high organic content above the mineralic deep soil), for example, *Eurhopalothrix elke* (Mezger & Pfeiffer 2010a), certain species of *Cerapachys* (Borowiec 2009) and *Pheidole schoedli* (Eguchi et al. 2006). For some species, it was not specified in which soil stratum they were collected, for example, *Secostruma* (Bolton 1988) and *Crematogaster masukoi* (Hosoishi et al., 2011). A new method for sampling soil ants in even deeper layers has been developed by Wilkie et al. (2007) in the Neotropics where it found species restricted to layers lower than 15 cm, but this method has not yet been applied in other regions; thus, better sampling of the soil stratum would also increase the species total. The forest canopies remain another “biotic frontier” even after decades of studies, because only a relatively small amount of the formicid material has been identified to species level from the lower canopy (e.g., Floren & Linsenmair 2005), while from the higher canopy few studies are known, including the sampling of ferns (Ellwood et al. 2009) and direct observation from canopy platforms (Tanaka et al. 2010).

A high percentage of Bornean species sampled in ecological studies can still not be identified; for example, in our recent large-scale study of soil and leaf litter ants (100 m² sampled, Mezger & Pfeiffer, 2011a), we could identify only 63 percent of species, although our study area in Gunung Mulu National Park is one of the most intensively surveyed areas on the island, from which many of the Dacetini described by Bolton (2000) were collected. One reason for the low proportion of identified species is the lack of comprehensive studies with identification keys to speciose genera like *Paraparatrechina*, *Camponotus* and *Anochetus*. Moreover, many of the tropical species are rare or very rare and rarefaction methods reveal that sampling efficiency in all ecological studies conducted in primary forests of Borneo, in the tree canopy as well as in the soil stratum, never reached more than 85 percent (e.g., Floren & Linsenmair 2000; Brühl et al. 2003; Mezger & Pfeiffer, in prep.); thus, leaving a large number of species undetected (Longino et al. 2002). Given the limited sampling effort and the rarity of species it is unsurprising that records of certain species remain scarce, for example, *Polyrhachis muara* has been described on the basis of two specimens (Kohout 2008), and the monotypic ant genus *Secostruma* is represented by a single worker from a soil core (Bolton 1988).
The low abundance of many species in tropical primary forests is demonstrated in studies of ant community ecology by steep rarefaction curves and the long tail of rare species in local species abundance curves (e.g., Floren & Linsenmair 2000; Brühl et al. 2003; Mezger & Pfeiffer, forthcoming). Bornean ant genera, with a few speciose genera and a long tail of genera with only one or two species, show an analogous pattern (Fig. 1). While some of the less diverse genera (e.g., Anoplolepis, Oecophylla and Paratrechina) contain very abundant species, many of them include rare species, indicating that in these cases evolutionary forces restrict local abundance as well as regional radiation of the species.

The median species-per-genus value in Borneo of only 2.0 indicates that half of the genera with valid species (49) have only one or two species. On the other hand, some of the genera present a very rich diversification. So, although the species:genera ratio in Bornean ants of 8.06 is low compared with that of the world’s ants (47.14, based on 14,095 species in 299 genera: Bolton 2010), it is similar to that of New Guinea (8.5) and higher than those of the Philippines (4.9) and temperate Mongolia (4.0). However, due to the low percentage of described species in certain ant genera, for Borneo at least, this ratio is likely to be a substantial underestimate.

A considerable percentage of the 389 species with types from Borneo are not recorded from other places and might be endemic to Borneo. In many cases, it is hard to assess whether a certain species is really restricted to this island or whether this just represents a collection bias, since many of the surrounding islands like Sumatra, Java and Sulawesi have been less intensively sampled and have received less attention from taxonomists than Borneo. But some better-studied taxa have been well sampled all over the region; thus, conclusions about their endemism are possible. Of the seven species of the conspicuous Dolichoderus cuspidatus-group, six are recorded only from Borneo despite collection trips to the Malay Peninsula, Sumatra and Java, as well as museum collection and literature surveys, and are most likely endemics to this island (Dill 2002). On the other hand, Pheidole shows a lower percentage of endemics; of the 56 species described by Eguchi (2001) from Borneo in a comprehensive study, only 12 seemed to be endemics.

Many Borneo-endemics are not evenly distributed over the whole island, but seem to be restricted to a certain area. Mountains like Gunung Kinabalu are prominent hotspots of endemism. However, making quantitative statements on this issue is difficult, since most sampling was conducted in a few locations with most of Borneo poorly sampled, so many “local endemics” might be sampling artefacts. Many of the Strumigenys and Pyramica species described by Bolton (2000) were only reported from one locality on Borneo. Other possible local endemics include the rare Anillomyrma tridens and members of the six Bornean monotypic genera Anomalomyrma, Bregmatomyrma, Ishakidris, Loweriella, Secostruma and Tetheamyrma that have been rarely documented. A question here is how many more such genera await discovery? Many other genera show an allopatric distribution on Borneo, with species restricted to certain localities, for example, the three species of the Euhopalothrix platisquama-group (Mezger & Pfeiffer 2010a) and the two species of the Cerapachys sexspinus-group (Borowiec 2009). Local-endemic species are especially endangered by habitat destruction and climate change. As nest temperature is an important niche factor for tropical ants (Mezger & Pfeiffer 2010b), higher temperatures due to global warming may endanger species in fragmented forest islands in the lowlands, as well as isolated species on mountain tops.

Little is known about the presence of taxonomically-cryptic ant species. Studies on the subgenus Decacrema of Crematogaster have shown that specimens of the same morphotype that had been gathered from a wide geographic range (West Malaysia and Borneo) were in fact species-complexes that differed widely in their DNA codes (Feldhaar et al. 2003). Camponotus rufifemur, too, may represent a cluster of several closely related species (F. Menzel, pers. comm.). Similarly, a high percentage of the valid subspecies may turn out to be true species. Ant subspecies have rarely been described in recent decades and all putative subspecies should eventually be reassessed by genetic investigations.

We took the opportunity to compare the species list from Borneo with those of New
Guinea (Janda 2010) and the Philippines (Alpert & General 2010). New Guinea is separated from Borneo and the Philippines by the Wallace Line, and this faunal border reduces the similarity of the fauna. However, at genus level, the faunal similarity of the three areas is quite high and even for species we found quite high similarity with the Philippine fauna. As comprehensive species lists of the ant fauna from the Malay Peninsula, Sumatra and Java are missing, it is currently impossible to compare the Bornean data with other Sundaland areas at species level. The most complete species list from Peninsular Malaysia is from Pasoh Forest Reserve where Malsch et al. (2003) collected 489 ant species belonging to 76 genera and nine subfamilies, although most specimens could only be identified to morphospecies level and sampling was from only a single location. When we compared this ant fauna at genus level with that of Borneo using the Sörensens Index, we found a value of 0.83, slightly higher than the generic similarity with the Philippines.

Taken together, the ant fauna of Borneo is of immense diversity and importance and our paper can only be a further step towards its full description. More intensive sampling at diverse locations on the island is necessary to get a more comprehensive idea about its entire ant fauna. Two-hundred-and-twelve years of ant research have still revealed only a portion of Borneo’s immense diversity. However, without a halt to the ongoing habitat destruction, many species of the Bornean rainforests will become extinct before they are known to science. This holds for ants as well as for all other organisms in this wonderful ecosystem. It is time for a change towards more responsible human behaviour if we want to conserve this treasure for future generations.

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Each citation is tagged with a number which refers to a number in Appendix 1.


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Appendix 1. List of species and subspecies of the Formicidae of Borneo. Given are the subfamily and the species names, including authors and publication year, the existence of type-material from Bornean locations, the numbers of references which prove a Bornean location, and remarks on some of the species. Nominate subspecies are not listed. Type-material: X denotes a holotype collected on Borneo, (X) stands for any other type collected from Borneo (e.g., syntype, paratype, also for subsequently described gynes), and for types of junior synonyms, collected from the island. Codes and remarks: ◆ picture or location data from Borneo listed at www.antweb.org, ○ picture or location data from Borneo listed at www.antbase.net, A = stored in ABNC, B = stored in BNHM. Reference numbers referring to species locations on Borneo are listed at the end of the respective references. Species descriptions are listed in the references list, but not necessarily noted as numbers. Data published after July 2010 are incompletely included. Data (n = 5) added after 28 February 2011 were only joined to the list, but not included in the text of the paper.

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**Dolichoderinae**

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**Ponerinae**

*Anochetus agilis* Emery, 1901          X ◆ B, 35, 40, 79, 124, 246
*Anochetus graeffei* Mayr, 1870         A, B, 123
*Anochetus incultus* Brown, 1987        ◆ B
*Anochetus modicus* Brown, 1978         ◆ 35
*Anochetus muzziolii* Menozzi, 1932      B
*Anochetus myops* Emery, 1893            ◆ B
*Anochetus princeps* Emery, 1884         ◆ B, 122, 34b
*Anochetus rugosus* (Smith, 1857)        (X) ◆ B, 35, 123, 202
*Anochetus tua* Brown, 1987              124
*Centromyrmex* Mayr, 1866               B, 122
*Cryptopone testacea* Emery, 1893        (X) ◆ 40, 252
*Diacamma holosericeum* (Roger, 1860)    40, 163, 246
*Diacamma intricatum* (Smith, 1857)     X ◆ 40, 163, 202, 246, 257
*Diacamma intricatum kershawi* Wheeler, 1919 | X | ◆ 40, 246 |
*Diacamma rugosum* (Le Guillou, 1842)    X ◆ ◆ A, 105, 150, 163, 202, 246
*Diacamma sculpturatum* (Smith, 1859)    123

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**Proceratiinae**

| Discothyrea Roger, 1863                              | ◊        | A                                                     |
| Probolomyrmex itoi Eguchi, Yoshimura & Yamane, 2006  |          | 64                                                   |
| Probolomyrmex maryatiae Eguchi, Yoshimura & Yamane, 2006 | X | ◊ A, 64                                               |
| Proceratium angulinode De Andrade, 2003             |          | 11                                                   |
| Proceratium banjaranense De Andrade, 2003            |          | 11                                                   |

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<td>Tetraponera nigra (Jerdon, 1851)</td>
<td>○ 202, 236, 246</td>
<td></td>
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<tr>
<td>Tetraponera nitida (Smith, 1860)</td>
<td>○ A, 236</td>
<td></td>
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<tr>
<td>Tetraponera nodosa Ward, 2001</td>
<td>236</td>
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<td>Tetraponera pilosa (Smith, 1858)</td>
<td>X</td>
<td>◆ ○ A, 203, 236, 246</td>
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<tr>
<td>Tetraponera polita Ward, 2001</td>
<td>236</td>
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