Chapter 2

Biogeography

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2.1 Introduction

Understanding the processes that have allowed ants to spread into and dominate so many different habitats is an active area of research involving analysis of their current distribution as well as historical and geographical factors that affect dispersal and radiation (e.g. Brady *et al*. 2006; Moreau *et al*. 2006). In this chapter, I examine global diversity patterns for present-day and fossil taxa, analyse taxonomic case histories using the genus *Crematogaster* and the subfamilies Pseudomyrmecinae and Dolichoderinae as examples, describe 'hotspots' of world ant diversity, and discuss how islands' species distributions serve as a model system for understanding the biotic evolution in a region and ant biogeography in general.

2.2 Global biogeographic patterns

If you want to travel the world to encounter as many ant species and genera as possible, where would you go? If you could only visit a few places, which biogeographic regions would you choose? Studies of global ant distribution patterns are providing answers to these types of questions.

There are currently a total of 290 extant ant genera (Appendix 1) and over 12,500 described extant species (Bolton *et al*. 2006; see also Chapter 1). Given the high rate of new species descriptions (Ward 2007c) and the large number of undescribed species in collections, the total number of ant species (described and undescribed) may be as high as 30,000. However, species are not randomly or uniformly distributed across the earth. Geography, geology, and climate all play a role in the diversification and spread of lineages. These factors explain how and why species and genera have assembled in a given region, and why endemic taxa are clustered in particular areas. As will be discussed in Section 2.6, species distributions, especially on oceanic islands, may also reflect an element of chance — the rare and fortuitous dispersal of a species from a source population.

On a global scale, ant fauna can be divided into biogeographic regions that contain endemic and closely related taxa and, at their boundaries, show rapid turnover of species (Figure 2.1). Deciding on the number of regions and their boundaries is arbitrary and open to debate (Cox 2001; Morrone 2002). Early researchers of birds and mammals defined zoogeographic regions somewhat subjectively, based on their intuition about how to interpret geographic patterns (e.g. Wallace 1855). They observed that the range boundaries of species and genera are generally coincident within regions. Today, more rigorous approaches to the characterization and interpretation of biogeographic history are possible based on more detailed information on the distribution of species and their relationships. However, there is still debate as to the best approach to establish the boundaries of regions (Morrone 2002). Finer subdivisions may contain more information, but are less useful as a general reference system.

The classical biogeographic partitions of Pielou (1979) are based mostly on vertebrates and plants and include seven regions: Nearctic, Neotropic, Palaearctic, Afrotropic, Indomalaya, Australasia, and

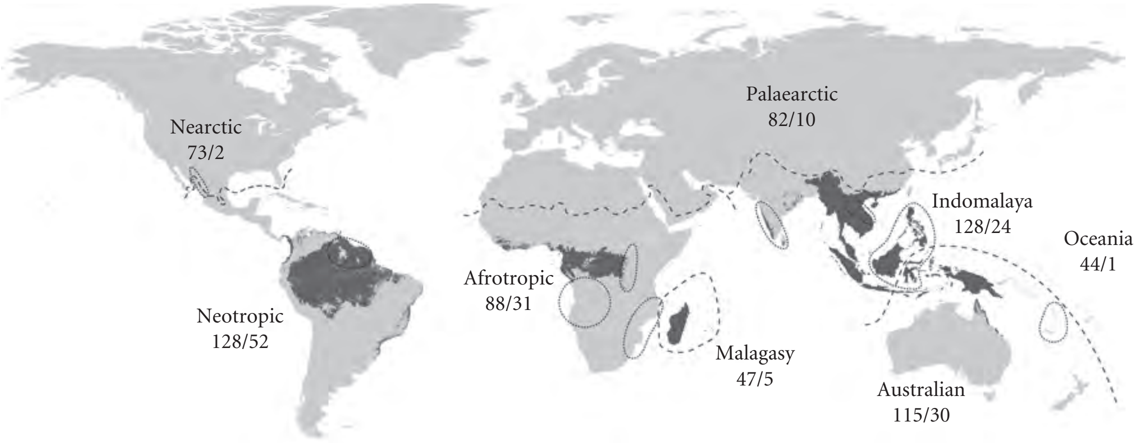

Figure 2.1 Biogeographic regions (delimited by long-dashed lines) and number of native ant genera and endemics. Biogeographic regions based on the classical regions of Pielou (1979) and Olson *et al*. (2001). Areas depicted in dark grey show exceptional diversity. Outlined areas (short-dashed lines) remain in need of exploration.

Oceania (excluding Antarctica, where no ants are found). Ant biogeographers such as Brown (1973) and Bolton (1994, 1995b) further divide them. Brown designates Madagascar as a distinct region from the Afrotropic, based on high levels of species endemism (>95%) (Fisher 2003). Bolton separates out Australia on the same grounds. In both cases, these divisions provide a practical advantage of generic lists and keys for regional analysis (Bolton 1994).

Defining regional boundaries is another challenge. Transitions between the historically isolated Nearctic and Neotropic faunas and the Palaearctic, Indomalaya, and Australian regions occur over a wide area, making it difficult to draw a definitive line between them. Most biogeographers use Wallace's Line, which runs just east of Bali, Borneo, and the Philippines, as the boundary between the Indomalaya and Australian regions (Figure 2.1). Bolton (1995b), in contrast, deviates from this conventional boundary and instead keeps the islands of southeast Asia (Malay Archipelago) together in the same region (Indo-Australian). While Bolton is correct that Wallace's Line is not a striking boundary for ant genera, it has been shown to be important at the species level. For example, Ward (2001) found that most of the 33 *Tetraponera* species do not cross Wallace's Line: 23 species were restricted to the Indomalaya region, while 7 species were confined to Australia, New Guinea, and adjacent islands. Only three species ranged through both the Indomalaya and Australasian realms.

With the above-mentioned caveats in mind, I evaluate the distribution of genera of living ants for the biogeographic regions outlined by classical biogeographers (Olson *et al*. 2001; Pielou 1979), with the addition of the Malagasy region, and compared them to Bolton's regions (1995b) (Table 2.1). A biogeographic summary based on species, rather than genera, is limited by our incomplete knowledge of species distributions (Dunn *et al*. 2007d) and a great number of undescribed species. However, Bolton's taxonomic catalogue (Bolton *et al*. 2006) does provide the country of origin for the type specimen(s) of each species. Based on these data, the rank of biogeographic regions in relation to the number of described species from each of the regions is shown in Table 2.1.

By all measures, the Neotropic is a regional hotspot for diversity, with the highest number of lineages (genera) and species, and the greatest number of endemic genera (Table 2.1). Not surprisingly, the larger, more isolated remnants of Gondwanaland (the Neotropic, Afrotropic, and Australia) show the greatest endemicity (Bolton 1995b). Overall, over half (53%) of all 290 genera, are restricted to one of the eight classical biogeographic regions.

Table 2.1 Comparison of the ranking of biogeographic regions based on number of genera, percentage of endemic genera, and complementarity, which maximizes the accumulation of the greatest number of genera, and number of described species between the classical biogeographic regions of Pielou (1979) and Olson *et al*. (2001) (classical) and those defined in Bolton (1995b). Number of plant species is based on Kier *et al*. (2005) and Qian and Ricklefs (2008).

Number of genera		**Endemic genera (%)**		**Complementarity**		**Number of described species**		**Plant species richness**
Classical	**Bolton**	**Classical**	**Bolton**	**Classical**	**Bolton**	**Classical**	**Bolton**	**Classical**
NEO (128)	NEO (128)	NEO (41)	NEO (41)	NEO	NEO	NEO	NEO	NEO
IND (128)	INA (122)	AFR (35)	AFR (35)	IND	INA	IND	INA	IND
AUS (115)	ORI (112)	AUS (26)	AUS (21)	AFR	AFR	AUS	AFR	AFR
AFR (88)	AUS (99)	IND (19)	INA (12)	AUS	AUS	AFR	PAL	AUS
PAL (82)	AFR (88)	PAL (12)	PAL (12)	PAL	PAL	PAL	AUS	PAL
NEA (73)	PAL (82)	MAL (11)	MAL (11)	MAL	ORI	NEA	ORI	NEA
MAL (47)	NEA (73)	NEA (3)	ORI (6)	NEA	MAL	MAL	NEA	MAL
OCE (44)	MAL (47)	OCE (2)	NEA (3)	OCE	NEA	OCE	MAL	OCE

Note: NEO = Neotropic, IND = Indo-malaya, INA = Indo-Australian, AUS = Australian (classical) Australasian (Bolton), AFR = Afrotropic, PAL = Palaearctic, NEA = Nearctic, MAL = Malagasy, OCE = Oceania, ORI = Oriental

The Malagasy region, a less isolated Gondwanaland remnant, still shows a remarkable degree of diversity relative to its small area, with more endemic genera than Oceania. Although the Palaearctic encompasses more than twice the land area of the Neotropic region, its diversity is just two-thirds that of the Neotropics, a reflection of its colder, drier, high latitude climate. Climatic conditions comparable to the Palaearctic are found in the Nearctic region, which is home to a similar degree of diversity when its relative isolation and smaller landmass is considered. Differences between faunas grow progressively less distinct as one moves between the Palaearctic and Indomalaya, and the Australasian regions.

Overall, however, patterns of global ant diversity adhere closely to patterns for other terrestrial fauna and flora, with the most diverse communities found in lowland tropical regions. Species richness accounts of plants (Kier *et al*. 2005 and references therein; Qian and Ricklefs 2008) rank the biogeographic regions similarly, with one notable difference. Ant species richness is relatively greater in the Australasian region than that of plants, suggesting more ant than plant diversity in the drier areas of the continent.

Gondwanaland endemicity is particularly striking in the Afrotropic and Neotropic regions. These two regions show no overlap among native ant species (Brown 1973). Of the 128 genera in the Neotropics, only 36 are found in the Afrotropics. However, this is unsurprising given the long, 100-million-year period of separation between Africa and South America (Ali and Aitchison 2008) and the ages of extant ant lineages, which generally emerged long after the breakup of Gondwanaland (Brady *et al*. 2006). These results suggest that it is unlikely that extant genera in South America were present when Africa and South America were connected (see Section 2.3).

While the era of ant exploration is clearly far from over, with many regions likely to yield treasures of undescribed genera and species (see circled areas in Figure 2.1), the overall species and genera richness patterns described here are likely to hold. Our growing understanding of ant relationships will further improve the analysis of biogeographic patterns. Phylogenetic studies, when combined with divergence times estimates, permit analyses of the origin, dispersal, radiation, and spread of taxa across regions. Section 2.4 includes three case histories where phylogeny was included in a historical biogeographic study.

2.3 Palaeogeographical distribution of fossil ants

Understanding how extant ant lineages arrived at their current distribution patterns requires a study of their origins and distribution history. This section examines what we know about ant history based on the fossil record (see also Chapter 1).

2.3.1 Geography

With almost 50% of extant genera restricted to just one of the biogeographic regions, were early ant ancestors equally isolated on different land masses? For early ants, where was the hotspot of diversity as compared to today's tropical lowland forest? Unfortunately, the geographic origins and patterns of early ants are somewhat obscure. The scarcity of early ant fossils challenges our ability to compare historical and current patterns.

The oldest known fossil ants are from French and Burmese ambers in the early-to-mid-Cretaceous period (Figure 2.2; see also Chapter 1). These are surprisingly rich, including at least seven distinct genera. The palaeoenvironment of the French amber is estimated to have been a subtropical rainforest (Perrichot *et al.* 2008a). Thus, these early ants already seem to exhibit a preference for moist and hot places. The contemporaneous occurrence of these genera implies that by the Albian (~105 Mya), ants had already significantly diverged and were widespread with multiple lineages co-occurring on the same continent. Unfortunately, our picture of ant evolution before the Albian is blank and lacks a single ant fossil. Because they were already diverse by the Albian, I share the view of Perrichot *et al.* (2008a) that eventually fossils will be found earlier in the Cretaceous.

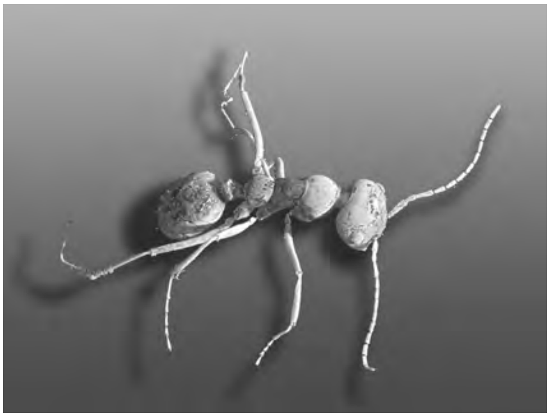

Figure 2.2 *Sphecomyrma* sp., Sphecomyrminae, from early Cenomanian amber of La Buzinie, Charente, SW France. Three dimensional virtual reconstruction in phase contrast synchrotron microtomography. (Image: Lak [CNRS/ESRF] / Tafforeau [ESRF] / Perrichot [Kansas Univ.] – ANR AMBRACE.)

The distribution of Cretaceous specimens demonstrates that ants had spread across much of Laurasia (today's northern hemisphere continents) early on in their evolution (Perrichot *et al.* 2008a). We cannot say much about their spread through Gondwana. Early ants are conspicuously absent from Gondwanan fossil deposits from the early to mid-Cretaceous. The first accurate record is a diverse set of Formicidae from Botswana dating slightly later from the Turonian (~93 Mya). The absence of Gondwanan deposits before the Turonian may reflect the limited extent of early ant habitat as well as the chance nature of locating fossils.

The findings from fossil taxa combined with phylogenetic divergence data suggest that the distribution of extant genera was not driven by Gondwanan vicariance events. The dating studies show that most subfamilies originated (stem group) after the breakup of Gondwana and in the late Cretaceous, and followed by within-subfamily diversification in the Palaeogene (Brady *et al.* 2006; Ward 2007c). These dating estimates imply that during the breakup of Gondwana (~100 Mya), the ant genera now found in South America, Africa, and Madagascar were not yet present. Thus, the current distribution of the army ants *Dorylus* (Africa) and *Eciton* (New World) cannot be a consequence of the breakup (cf. Brady 2003; Brady *et al.* 2006). Nor can the Gondwanaland distribution of one of the early branching lineages of extant ants, *Amblyopone* and *Mystrium*, found in just a handful of pockets around the world, be attributed to the breakup. Instead, the ages of these four lineages imply that their current distribution is a product of dispersal, radiation, and spread of taxa across these isolated biogeographic regions.

The overall results are that the modern ant collector is dealing with a fauna that arose less than 50 or 60 Mya. For example, one peculiarity that emerged in the early Eocene (~50–55 Mya) was the giant ants (*Formicium giganteum*), subfamily Formiciinae (Lutz 1986, 1990, 1992). Ant collectors of today can only dream about what it might be like to collect these extinct lineages. The common use of a pooter (aspirator) would not have been advised to gather these ants. Workers are not yet known, but full-bodied queens have been found in Germany and Tennessee (USA) and males of one species in Germany. These giants were likely carnivorous and grew up to 5.5 cm, with 13 cm wingspans that were larger than those of some modern hummingbirds.

2.3.2 Geographic patterns of ant extinction

The fossil record has provided evidence that genera and subfamilies with a modern restricted distribution may represent the survivors of a lineage that at early times was more widespread. For example, the sole surviving representative of the subfamily Aneuretinae, *Aneuretus simoni*, is found exclusively in central Sri Lankan rainforest and is the sister group of the Dolichoderinae (Brady *et al*. 2006). During the Mesozoic and early Palaeogene, aneuretines were distributed widely in North America and Eurasia (Dlussky and Rasnitsyn 2003; Engel and Grimaldi 2005). What led to the extinction of other aneuretines? Engel and Grimaldi (2005) propose the Eocene–Oligocene (~35 Mya) climatic shift that altered biogeography of numerous insect lineages (Grimaldi and Engel 2005). It is unclear how *A. simoni* was able to survive the factors underlying the extinction of its relatives.

The Myrmeciinae were also much more diverse historically than their modern distribution would indicate. Present-day native Myrmeciinae are restricted to Australia and New Caledonia. Though fossil records for the subfamily are restricted to the Eocene, the subfamily included a number of genera distributed throughout the world, including fossils from North America, South America, and Eurasia (Archibald *et al*. 2006; Dlussky and Rasnitsyn 2003; Ward and Brady 2003).

Genera also show patterns of extant lineages occupying restricted ranges compared to their ancestors. *Leptomyrmex* is today found only in New Guinea (and nearby islands), eastern Australia, and New Caledonia, but traces of one fossil species were found also in Central America (Dominican amber) (Baroni Urbani and Wilson 1987).

We understand very little about why some representatives of lineages survive while others do not (e.g. *Nothomyrmecia*, the only living representative of the ancient lineage Prionomyrmecini; see Box 2.1). For some taxa, at least, nesting site appears to have played a role. The proposed earliest branching lineages of extant ants include the subfamilies Leptanillinae and Martialinae (Brady *et al*. 2006; Rabeling *et al*. 2008). In both these subfamilies, extant species are thought to forage and nest underground. It is possible that the taxa that have persisted today were exclusively subterranean. Their underground habitat could have provided protection from competitors, climatic shifts, or other environmental changes that drove their relatives to extinction (Rabeling *et al*. 2008).

2.4 Phylogenetic-based biogeography

Analyses of phylogenetic relationships among ants can yield far more than just lineage information. Considered together with habitat requirements and mutualistic relationships, they can shed considerable light on the regional history of climatic, tectonic, and other geographic shifts. I have examined three case studies: the genus *Crematogaster*, where historical analysis sheds light on geographic and climactic events; and the subfamilies Pseudomyrmecinae and Dolichoderinae, where phylogenetic patterns correlate with geography.

2.4.1 *Crematogaster*

One example of historical biogeography is the phylogenetic study of mutualistic myrmicine ants of the genus *Crematogaster* in Sundaland, southeast Asia (Quek *et al*. 2007). Sundaland is an extension of the continental shelf of southeast Asia that

Box 2.1 The remarkable rediscovery of the Dinosaur Ant, *Nothomyrmecia macrops*

Robert W. Taylor

The 'Dinosaur Ant', *Nothomyrmecia macrops*, is considered to be perhaps the most archaic living formicid. It is related to the Australian bulldog ants (*Myrmecia*), to the Baltic amber *Prionomyrmex*, and the Argentinian fossil *Ameghinoa* (Ward and Brady 2003). The significance of this morphologically 'primitive' ant was recognized by its describer John Clark (1934). Brown and Wilson (1959b) reviewed its known history, making the prediction that such a pale-coloured, large-eyed creature must be nocturnal.

The first two known worker specimens were collected in 1931, almost certainly on the remote 120 km bush track between Balladonia Station and Mount Ragged in southeast Western Australia. Several specifically targeted expeditions subsequently failed to rediscover the species, which to date has not been collected again in Western Australia, but is now known to range from Poochera in South Australia, southeastwards into the Eyre Peninsula, and west towards the Nullarbor Plain. *Nothomyrmecia* was finally rediscovered in 1977, almost 1,200 km to the east of its original collection, near the hamlet of Poochera, South Australia; a Mecca for myrmecologists, and a place now targeted by many ecotourists.

The rediscovery of *N. macrops* is a tale of unexpected triumph. Five team members, including Don Colless, Murray Upton, John Lawrence, John Feehan, and myself, set out to search the distant Mount Ragged track in Western Australia for *Nothomyrmecia*, in a last-ditch Australian attempt to find the ant, following word that a well-financed expedition (his third) was being planned by the noted American myrmecologist William L. Brown. Two days westwards from Canberra, we were delayed at Wudduna, South Australia, for vehicle repairs. I distributed colour slides of the *Nothomyrmecia* types to the group, anticipating the coming rediscovery, which unbeknown to us was fatefully then only hours away. Later, while refuelling at Poochera, we decided to make camp nearby, still many hours short of the originally projected campsite that night.

Colless valiantly proposed collecting in the camp area, to which everyone else reluctantly agreed. I left the caravan last to meet an icy south-west wind inauspicious for ant activity. After about five fruitless and begrudged minutes, I moved back towards the warmth when my headlamp caught a *Eucalyptus* trunk about 15 m from the caravan. There, on the tree trunk was a spotlighted *Nothomyrmecia* worker! The amazing serendipity of the night was complete. I rushed to the caravan where a light sheet was in operation and famously proclaimed: 'The bloody bastard's here.' We collected more workers from the same tree, and yet some more the following morning from the ground nearby. Later, following an unsuccessful search at Mount Ragged, I flew to Canberra from Perth, and was back at Poochera by mid-November with then Sydney University student Phil Ward to collect the first live colonies (Taylor 1978). The rest is history.

Nothomyrmecia has the usual 'formicid' attributes (Figures 2.1.1 and 4.2), including metapleural glands, dealation by recently mated queens; an apterous, mesosomally reduced worker caste, which is a generation younger than the colony queen; elbowed antennae; a petiolate waist; and a non-cellular nest in which eggs, larvae, and pupae are not segregated in individual cells. Its 'primitive' features include the powerful (and painful) sting, the low dimorphism between queens and workers, and the presence of worker ocelli and pupal cocoons. Specialized features are the obligate nocturnal foraging activity, the peculiarly reduced wings of virgin queens, and the ventral rather than dorsal abdominal stridulatory organ, a structure almost unique among the Hymenoptera. The diploid chromosome number $2n=94$ is the second highest known for any non-polyploid animal (Imai *et al*. 1990).

continues

Box 2.1 continued

Figure 2.1.1 *Nothomyrmecia macrops* queens, worker (lower left), and pupae. (Photo: Robert W. Taylor)

Founding queens cohabit in groups of up to four in nests excavated in the soil. They forage like workers during this period, and are reduced by aggression to one when the first daughter workers appear. Nests extend nearly a metre below ground as colonies grow to contain up to 200 workers. Lone foragers gather insect prey on trees near their nests, and individually return to the same tree, night after night. The contents of waste middens accumulated deep in the nests consist largely of hemipteran and dipteran remains, with very few beetle or lepidopteran fragments. Proteinaceous food is supplemented by sugary liquids, including honeydew deposits (hemipteran excretions). Navigation involves exceptional visual acuity using the tree canopy pattern against the night sky, and possibly also polarized-light sky patterns, as a map. All foragers depart nests within the hour following nightfall. Successful huntresses return during the night, while those without prey return in numbers at dawn. Researcher Birgit Greiner has commented that their eyes are so strongly dark-adapted that they are essentially blind in daylight.

includes Borneo, Malaya, and Sumatra. During the Pliocene (~1.8–5 Mya), climate fluctuations caused wet periods to alternate with regimes of cooler and drier weather. During the same era, rising sea levels alternately inundated and reconnected the Sunda Shelf landmasses. Phylogenetic studies of *Crematogaster* have yielded insights into the climatic and geographical changes that accompanied these events.

One clade of *Crematogaster* ants, the subgenus *Decacrema*, evolved an extremely close relationship with trees of the *Macaranga* genus in Sundaland. The ants live exclusively in the hollow stems or domatia of the trees and consume food bodies in the leaves. In exchange, the colony defends the plants against encroachment by other animals and vines. The trees themselves are restricted to areas of continuously wet rainforest, and cannot withstand drought or seasonality. For this reason, the evolutionary relationships among *Crematogaster* ants can serve as a surrogate index of climate change in the Sunda Shelf.

Molecular phylogenetic studies of the *Decacrema* ant complex indicate that of the three locations in Sundaland, Borneo contains by far the greatest number of lineages, suggesting it is the home of the ancestral species. Chloroplast DNA studies point to a similar origin for *Macaranga* trees. Meanwhile, the highest lineage diversity of ants on all three islands is found on mountaintops. This finding indicates that the ants in high-elevation rainforests enjoyed moist conditions throughout the Pleistocene, allowing them to spread and diversify without interruption. By contrast, cooling and drying climate shifts shrank the rainforest cover on lower elevation slopes, and reduced ant diversity.

The relationships among Sumatra, Malaya, and Borneo ant lineages have also suggested times when these areas were connected. The relative ages of Sumatra and Malaya ant lineages that are most closely related to Borneo lineages likely reflect periods of low sea level when land bridges connected some areas but not others. Meanwhile, lineages with constricted ranges or patchy distributions among the three sites likely reflect past dramatic range reductions that severed shelf connections and turned these areas into refugia for rainforest and ants alike.

2.4.2 Pseudomyrmecinae

The ant subfamily Pseudomyrmecinae comprises big-eyed arboreal ants that are widespread in tropical and subtropical regions throughout the world and number about 300 species. Most of these species colonise dead twigs, stems, and branches, although about 40 species have obligate mutualistic relationships with domatia-bearing plants. In their study of the subfamily, Ward and Downie (2005) used a combination of molecular data and morphology to investigate the biogeography and biological evolution of the Pseudomyrmecinae.

The current distribution of these ants suggests that they originated in a portion of Gondwanaland during the mid-Cretaceous. Molecular genetics point to an exceptionally long stem lineage that was initially marked by limited diversification. The phylogenetic analyses of Ward and Downie (2005) indicate an origin in the Old World Tropics (paraphyletic *Tetraponera*) followed by dispersal to the New World Tropics and subsequent diversification (*Pseudomyrmex*). Therefore, much of this species divergence took place after the continents had broken up and reached their current locations. Using results that show *Tetraponera* as a paraphyletic grade at the base of the Pseudomyrmecinae, Ward and Downie (2005) proposed that the ancestral area for the genus is Indo-Australia and not Africa as proposed by Ward (2001).

The current pattern of pseudomyrmecine diversity resembles geographic trends seen in other taxa inhabiting both Neotropical and Palaeotropical forests. The greatest number of species (200+) is found in the Neotropics (Table 2.1). This region includes a wide variety of habitats due to active mountain building and other geographic characteristics, which may explain this proliferation of species. The greater diversity of the region's habitats, combined with a relatively consistent climate and large area, may have provided conditions ideal for diversification. The lowest number of Pseudomyrmecinae species, 25, is found in Africa, a landmass that has experienced high rates of extinction due to large climate shifts, and where tropical forests cover a smaller area at relatively high elevations (~500 m above sea level).

2.4.3 Dolichoderinae

The subfamily Dolichoderinae is a cosmopolitan group of ants known for using chemical defences and sheer numbers to dominate ant communities. The 840-plus species in the group include several of the world's most successful invasive ants, including the Argentine ant (*Linepithema humile*), the ghost ant (*Tapinoma melanocephalum*), and white-footed ants (*Technomyrmex albipes, T. difficilis*, and *T. vitiensis*). Fossil records suggest that the dolichoderines declined in the northern hemisphere starting in the late Eocene, although their abundance and diversity have remained strong in the southern hemisphere, especially in Australia.

Combining both fossil and molecular data in a dispersal-vicariance analysis (DIVA), P.S. Ward and colleagues (unpublished) address the historical biogeography and diversification of the group. Their work indicates that the crown group Dolichoderinae arose in the Palaeocene (~65 Mya) and was preceded by ~30 million years of stem lineage evolution (and presumed extinction).

Their work had identified four main clades within the subfamily Dolichoderinae. Based on the DIVA, the crown group Tapinomini, the sister group of all other extant dolichoderines, arose in the Afrotropics < 60 Mya. The sister to the remaining dolichoderines, Bothriomyrmecini is estimated to have their crown group origin in the Indomalaya region. Both Tapinomini and Bothriomyrmecini have remained diverse in the Palaeotropics, but a few representatives have colonised the Nearctic and Neotropical regions (e.g. species in the genera *Bothriomyrmex, Technomyrmex, Liometopum*, and *Tapinoma*). The genus *Dolichoderus*

(=tribe Dolichoderini) was not evaluated in the analysis but the crown group is currently widespread, being absent only from the Afrotropics. The remaining lineage, tribe Anonychomyrmini, originated and diversified in the Neotropics into hundreds of species that now include groups in North America (*Forelius, Dorymyrmex*) and multiple dispersal events from South America to Australia during the mid-Tertiary. One of these dispersals, by the common ancestor of *Linepithema* and *Iridomyrmex*, led to a spectacular radiation that has produced several of Australia's most dominant ant species (Andersen 1995). Thus, the arrival, diversification, and dominance of dolichoderines in the Australian region occurred later than in other parts of the world. Interestingly, the close relationship of the dolichoderine fauna in Australia to *Linepithema* may explain the limited invasion by the human-dispersed Argentine ant (*L. humile*) over the last 100 years.

2.5 Hotspots: ants are more diverse in lowland, low-latitude forest

The world's most diverse ant communities tend to reside in low-elevation, low-latitude forests. In general, there is a strong latitudinal gradient in species richness, with tropical latitudes containing far more species than temperate zones (Ward 2000). Possible factors driving this pattern, discussed in detail in Chapter 3, include differences in temperature and the faster pace of species diversification in the tropics (Allen *et al*. 2006; Kaspari 2004). The warmth and higher predation rates of lowland tropical areas are correlated with a reduction in colony mass and an increase in ant abundance (Kaspari 2004).

The large size of lowland tropical forests further bolsters ant species richness in this biome (Rosenzweig 1995). Both the Amazon of South America and the Congo Basin rainforests of Central Africa are distributed in relatively large, unbroken blocks inhabited by relatively widespread species. Even the island of Madagascar contains a strip of eastern wet tropical forest that stretches for nearly 1,500 km from north to south. The continuity of these habitats helps sustain high levels of species diversity.

In general, ants have difficulty in tolerating cold and wet climates. In tropical regions, species diversity drops off in montane forest (Brown 1973; Fisher 1999b; Kaspari *et al*. 2004; Malsch *et al*. 2008). Ants are absent above about 2,300 m in all closed-canopy broadleaf forests, even those located in the tropics. However, they can be found at altitudes over 3,500 m in the open ground of the Andes or Himalayas (Brown 1973). Kaspari *et al*. (2000a, 2004) discuss the role of temperature in global ant patterns. But few studies address the factors behind the steep decline of ant species richness with increasing elevation and the general restriction of ants to relatively low altitudes in the tropics. Malsch *et al*. (2008) studied the biotic and abiotic factors in parallel among ground and lower vegetation ant communities along an elevational gradient. The study site consisted of evergreen tropical rainforest on Malaysia's Mount Kinabalu. They demonstrated that the steep decline in ant species richness with increasing altitude was correlated with several factors: (*a*) temperature decrease; (*b*) high humidity (comprising the relative humidity of the air, fog, rain, and waterlogging); (*c*) scarcity of nesting space; and (*d*) scarcity of nutritional resources. Overall, they found temperature to be the fundamental factor modulating other abiotic and biotic resources that determine this pattern. Ground temperature within closed-canopy forests is more likely to drop below the threshold necessary for ants to forage or develop efficiently (Brown 1973), reinforcing the idea that lowland tropical forests foster the most ideal conditions for ants.

Patterns of richness along elevational gradients are now of particular interest in light of climate changes (Deutsch *et al*. 2008). Janzen (1967b) proposed that tropical mountain passes are more effective barriers to dispersal than temperate-zone passes of equivalent altitude. He argued that because annual variation in ambient temperature at any site in the tropics is relatively low, it not only reduces seasonal overlaps in temperature between low- and high-altitude areas, but also selects for narrow temperature tolerances. As a result, tropical lowland organisms experience mountain passes as higher, more insurmountable barriers to dispersal than more temperate-zone species. This tendency in turn favours smaller species distributions such as those seen among tropical ants, and an increase in species turnover in ant assemblages along elevational gradients.

Climate change will favour organisms that can quickly acclimate, adapt, disperse, or change their behaviour (Deutsch *et al*. 2008). As Janzen suggested, the greatest biological diversity occurs in the tropics where change (e.g. rapid adaptation to climate change) is the hardest. Unlike deforestation, which is obvious and often noisy, climate change may drive tropical insects into silent extinction. But for ants that dominate the lowland forest, such as army ants, there is another point to consider. Once limited in elevation by wet and cold, these predatory insects will move to now warmer and less-cloudy higher elevations. At loftier elevations, they will encounter and threaten many groups such as beetles in the families Carabidae and Staphylinidae that are unaccustomed to competition with ants. To explore the potential impacts of climate change, ant communities along elevation gradients, especially at the cloud forest transition, should be monitored.

2.6 Islands

Islands offer a particularly clear lens through which ant biogeography can be viewed. The early studies of ants on islands (Caribbean, Melanesia, and Polynesia) by Wilson were of particular influence in the development of island biogeographic theory (MacArthur and Wilson 1967). Worldwide, more than half of the estimated 30,000 species of ants remain undescribed, a clear impediment in the study of biogeographic patterns. However, on the other hand, islands are much smaller in area and harbour fewer species than continents, making exhaustive inventories of their ant species possible. Careful study of this more limited species assemblage, combined with an array of islands differing in age, size, and isolation, can shed light on processes that affect ant composition, dispersal, extinction, and radiation. This natural laboratory, however, has been damaged and continues to be at risk. Increased habitat fragmentation, and the accelerated pace of ant species introductions, threaten endemic island ecosystems worldwide (Abbott 2005, 2006; Fisher 2005; Lach 2008b; O'Dowd *et al*. 2003; Underwood and Fisher 2006). Lowland tropical island faunas are especially susceptible to introduced ants; ant faunas that have been eradicated or severely reduced will complicate the analysis of biogeographic patterns.

2.6.1 Chance dispersal

The composition of the ant fauna on any particular island typically reflects the age, size, and relative isolation of the island (Figure 2.3). Ants often reach oceanic islands via accidental 'sweepstake routes' (Wilson 1988). As a result, even neighbouring islands tend to have unique assemblages of ant species. Ants in the sweepstakes face a low success rate, but those that successfully establish themselves enjoy a huge potential pay-off. Species that gain a foothold on a large island have the opportunity to radiate and fill many empty ecological niches.

Ants can arrive at islands via any of four common dispersal routes. A newly inseminated winged queen might be blown across the open ocean to distant shores. An entire ant colony might raft to an island inside a rotten log. Land bridges to other continents can be exposed during periods of low sea level. Lastly, ants are well adapted for transport by unwitting humans (Holway *et al*. 2002a; Wetterer 2006; Wilson 2005).

An island's size and geography determines much about its ant diversity (Figure 2.3). It is the primary factor driving whether or not dispersing ants can land and establish a foothold. Larger islands offer bigger targets for wayfaring ants to hit and more diverse habitats to occupy. The world's three largest tropical islands, New Guinea, Borneo, and Madagascar, have more endemic ant genera and species than any other islands on earth (Fisher 2009). While most island ants tend to originate from adjacent continents, prevailing winds and currents will also affect the sources of colonisation. Though Madagascar is much closer to Africa, a few of its ant lineages are related to taxa from Asia, where prevailing currents originate (Fisher 2000, 2003). Island age, too, plays a role in colonisation, as older islands offer ants more time to arrive and colonise. Moreover, the existing ant community, vegetation, and habitat determine whether new ants can survive and/or proliferate.

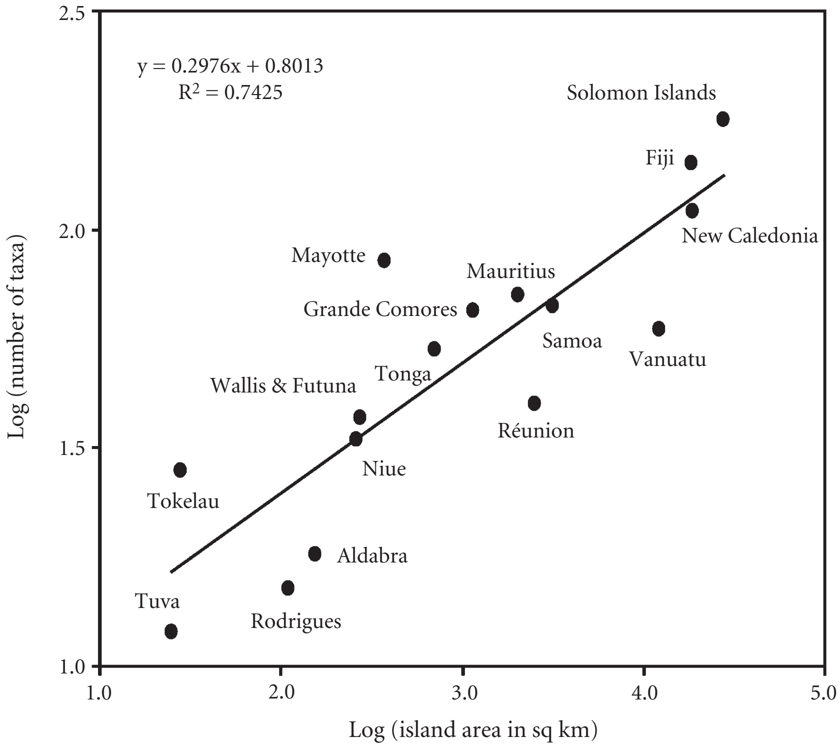

Figure 2.3 Log-linear regression analysis of ant species richness versus area of islands in the Pacific Ocean and southwest Indian Ocean. Though the size of an island is important, variation in species richness also reflects the age and relative isolation of the island. For example, Mayotte's proximity to Madagascar and great age (7.7–15 million years, Nougier *et al*. 1986) may explain the high number of species on the island. Data from Abbott *et al*. (2006), Ward and Wetterer (2006), and www.AntWeb.org.

The sweepstakes model of colonisation is exemplified by the pattern of ant diversity across the Antilles. This New World archipelago arcs across the Caribbean in a chain of more than 7,000 islands (Wilson 1988). While the smaller islands have fewer endemic species, those islands farthest from the mainland have fewer ant genera. In fact, few to no endemics live on Caribbean islands under 1,000 km^2, with one exception. Trinidad, located just 7 miles from mainland Venezuela, has an ant fauna characteristic of South America. Its species assemblage includes 17 genera widespread on the continent but absent from the rest of the Antilles.

Hawai'i offers a far more extreme example of biogeographic forces at work. A young and extremely isolated island chain, it is one of the few places on earth that lacks native ants. Since the arrival of humans, however, >50 ant species have been established. Many of these are extremely invasive and have devastated the islands' native insect faunas (Krushelnycky *et al*. 2005b).

Approximately midway between Hawai'i and New Zealand is the Pacific island nation of Tokelau. Though Tokelau is located at the hypothesized limit of native ants in the Pacific, a surprising number of tramp ants have assembled in a very small area. Tokelau consists of three isolated low-lying oceanic atolls which comprise 11 km^2 of terrestrial habitat, making it the nation with the world's smallest land area. Intensive sampling on the atolls recorded 28 ant species, with perhaps no natives or endemics, but a recently assembled community of human-dispersed tramps (Abbott *et al*. 2006).

At the opposite end of the age and diversity spectrum lies Madagascar, a very old island long isolated in the south-west Indian Ocean. Above 95% of its more than 1,000 ant species are endemic to the island, having arrived from Asia and Africa after Madagascar had been split off from Gondwanaland over 120 Mya (Fisher 2003).

2.6.2 Radiation

The relative paucity of insect species and the availability of empty niches on islands tend to encourage adaptive radiation among new arrivals (Zimmerman 1970). Larger islands may contain more diverse habitats and more niches to fill, encouraging the evolution of more endemic species. By the same token, older islands afford established species some additional time to diverge. For example, Cuba and Hispaniola, both relatively large islands, provided ideal platforms for endemic radiations of the genus *Temnothorax*. *Temnothorax* now constitute more than 25% of the ant fauna in Cuba alone and occupy habitats ranging from soil to limestone crevices and epiphytic plants (Wilson 1988). The biological diversity of this group is comparable to the range usually seen in several genera.

On Madagascar, ant genera (*Camponotus, Cerapachys, Hypoponera, Pheidole, Strumigenys*, and *Tetramorium*) demonstrate high levels of radiation (Fisher 2003). The morphological and niche diversity represented within *Cerapachys* alone is stunning, with some species having developed characteristics more typical of African army ants.

The composition of ants on an island at the time of arrival of a new species likely influences radiation as well. The lack of dominant mainland ants (e.g. army ants) on Cuba, Hispaniola, and Madagascar may have helped new species persist and radiate.

2.6.3 Taxon cycle

Based on studies of ants on the islands of Melanesia, Wilson (1959, 1961) proposed that species pass through 'taxon cycles', phases of expansion, and contraction in distribution accompanied by habitat shifts. He observed that expanding taxa tended to be recent arrivals that occupy coastline habitats. Wilson suggested that subsequent arrivals push species that arrived earlier farther inland and higher in altitude. As a result, older and endemic species are more likely to have fragmented ranges that consist of interior, montane habitats.

Because the taxon cycle is an historical model, an assessment of the model requires phylogenetics-based biogeographic methods to reconstruct the past history of events. Based on a phylogeographic analysis, the taxon cycle model has been supported in some studies, for instance of birds in the Lesser Antilles (Ricklefs and Bermingham 2002). No such study has been conducted for ants.

Though phylogenetic studies were not conducted, Fisher and Smith (2008) document an interesting pattern in the genera *Anochetus* and *Odontomachus* on the island of Madagascar that could be evaluated in the context of a taxon cycle model. In both genera, one or two species are restricted to higher elevation fragments, while another one or two species are widespread across lowland habitats. In both cases, the widespread species belong to groups found in Africa, while the restricted species are most similar to groups found only in Asia. An historical study is needed to evaluate if the African species-group taxa colonised after the Asian species-group taxa. If so, the first colonists of the lowlands may have been gradually pushed up into montane forest by new incursions of African species.

2.6.4 Turnover

The composition of ant species can vary considerably across an island's history. The primary forces that affect island biogeography — size, isolation, and habitats — also exert great influence on species turnover through time. Because islands are small and more prone to climate and colonisation shifts, species turnover among island ants can be surprisingly rapid. On Hispaniola, amber fossils indicate that 20 Mya, the island's ant fauna was closely related to the continental fauna of México (Wilson 1988). During this time, Hispaniola and its Greater Antilles neighbours were all located much closer to the mainland. But of the 38 genera and subgenera found in Dominican amber, only 22 persist today on Hispaniola. The farther the island travelled from the mainland, the more taxa were lost. Far from sources of new ants, few species arrived. Highly specialized species or those less able to establish themselves on new ground were the most likely to disappear. Volcanism, climate shifts, inundations, and other large-scale changes have caused similar effects on species turnover on other islands.

2.7 Future directions

Lack of a well-resolved phylogeny for many ant clades together with taxonomic uncertainties at the species level have limited the progress of understanding ant biogeography. With only an estimated 50% of ant species described, there is still a great need for species exploration and description. The recent discovery of *Martialis* demonstrated that new discoveries can shed light on the general pattern of ant evolution and radiation (Rabeling *et al*. 2008). Biogeographic studies will further benefit from these new species discoveries. Most importantly, studies that incorporate molecular phylogenies with divergence times estimated using previously established calibration points from fossil taxa will be necessary to understand the origin, dispersal, radiation, and spread of taxa across isolated biogeographic regions. Island systems, such as the southwest Indian Ocean islands, offer a model for exploring biogeographic questions. Because islands are smaller and often show a simplified ecology consisting of fewer species whose arrival can be dated, some questions can be easier to address than in larger, more complex, continental ecosystems. These questions include: (*a*) How many colonisation events occurred for each genus? (*b*) Did islands serve as stepping stones in dispersal? (*c*) What was the time frame for dispersal events?

The growing availability of standardized, geotagged data on ant distributions gathered from around the world (i.e. www.AntWeb.org) combined with enhanced geographic tools (e.g. Google Earth) will facilitate exploring fundamental questions regarding the distribution and history of ants on this planet. Geographic tools help visualize the role of topography, moisture, vegetation, and other environmental layers on species differentiation. The next technological challenge will be to juxtapose evolutionary relationships and distribution information atop geographic data. Such an online visualization tool will help reveal relationships among speciation and geographic barriers, connections to environmental conditions, and shifts in species over time.

The historical study of species distribution and how species have changed over time will also become increasing important as we try to understand how species will respond to climate change. We lack answers to simple questions about how the biota will respond to these new climate regimes. We do not understand how fast animals are changing their ranges, where they are moving, or which components of ecological communities (e.g. terrestrial versus arboreal arthropods) are most vulnerable to extinction. Answers to these questions are necessary for formulating adaptation strategies to minimize the impacts of global climate destabilization. One approach to predicting the impact of climate change is to evaluate how communities have changed in the past. Knowing how communities changed during past climatic shifts may be our best hope in mitigating current changes.

2.8 Summary

The present-day distribution of ants reflects the influence of geography, geology, and climate on the origin, diversification, and spread of a lineage. Though the process is complex, often difficult to reconstruct for a given taxon, and limited by the high number of undescribed taxa, two important overall patterns emerge: taxa are neither randomly nor uniformly distributed across the earth, and endemic taxa are clustered in particular regions. The greatest diversity is found in the tropics and the Gondwanaland fragments of South America, Africa, and Australia, which have the highest percentage of endemic genera, and where remarkable hotspots are found in moist lowland and low-latitude forests.

Approaches that combine exhaustive inventories, taxonomic revisions, and phylogenetics will enable a more rigorous approach to the study of biogeography. A newer approach, incorporating fossil records into studies of molecular divergence, shows promise for clarifying the ancient and relatively rapid origins of ant genera.

The rapid rate of ant species discovery continues to add nuance and critical missing links to the ant family tree.

Islands offer excellent model systems to explore outstanding questions of ant biogeography. One system with great potential includes the southwest Indian Ocean islands of Comoros, Madagascar, the Mascarenes, and the Seychelles. This region is diverse in origin, represented by coralline, volcanic, and Gondwanaland fragments. Ranging in age from 15,000 to 120 million years, the islands vary widely in size, degree of isolation, and habitat types. Such historical and geographic diversity makes these islands an ideal place to explore the relative impact of biogeographical factors on species diversity.

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Appendix

The distribution of ant genera across eight biogeographic regions. The table is a compilation of many published works, especially Bolton (1995), Brown (1973), Fisher (1997), and museum records. The biogeographic regions are the same as those defined by classical biogeographers (Olson *et al.* 2001; Pielou 1979). For each genus, "0" indicates absence and "1" indicates presence in that biogeographical region. Genera known only from probable tramp or introduced species in a given region are noted in [] but not included in the totals. I have not recorded all tramp species in all biogeographic regions, but have made efforts to note the most common recorded. NEA: Nearctic; NEO: Neotropical; AFR: Afrotropic; MAL: Malagasy; PAL: Palearctic; IND: Indomalaya; AUS: Australian; OCE: Oceania. It should be noted that because genera are constantly being revised, changes to the listed genera are likely in the future.

Genus	Subfamily	NEA	NEO	AFR	MAL	PAL	IND	AUS	OCE
Acanthognathus	Myrmicinae	0	1	0	0	0	0	0	0
Acanthomyrmex	Myrmicinae	0	0	0	0	0	1	1	0
Acanthoponera	Heteroponerinae	0	1	0	0	0	0	0	0
Acanthostichus	Cerapachyinae	1	1	0	0	0	0	0	0
Acromyrmex	Myrmicinae	1	1	0	0	0	0	0	0
Acropyga	Formicinae	1	1	1	1	1	1	1	1
Adelomyrmex	Myrmicinae	0	1	0	0	0	0	1	1
Adetomyrma	Amblyoponinae	0	0	0	1	0	0	0	0
Adlerzia	Myrmicinae	0	0	0	0	0	0	1	0
Aenictogiton	Aenictogitoninae	0	0	1	0	0	0	0	0
Aenictus	Aenictinae	0	0	1	0	1	1	1	0
Agraulomyrmex	Formicinae	0	0	1	0	0	0	0	0
Alloformica	Formicinae	0	0	0	0	1	0	0	0
Allomerus	Myrmicinae	0	1	0	0	0	0	0	0
Amblyopone	Amblyoponinae	1	1	1	1	1	1	1	[1]
Ancyridris	Myrmicinae	0	0	0	0	0	0	1	0
Anergates	Myrmicinae	1	0	0	0	1	0	0	0
Aneuretus	Aneuretinae	0	0	0	0	0	1	0	0
Anillidris	Dolichoderinae	0	1	0	0	0	0	0	0
Anillomyrma	Myrmicinae	0	0	0	0	0	1	1	0
Anisopheidole	Myrmicinae	0	0	0	0	0	0	1	0
Ankylomyrma	Myrmicinae	0	0	1	0	0	0	0	0
Anochetus	Ponerinae	1	1	1	1	1	1	1	1
Anomalomyrma	Leptanillinae	0	0	0	0	1	1	0	0
Anonychomyrma	Dolichoderinae	0	0	0	0	0	1	1	0
Anoplolepis	Formicinae	0	1	1	[1]	1	[1]	[1]	[1]
Aphaenogaster	Myrmicinae	1	1	0	1	1	1	1	1
Aphomomyrmex	Formicinae	0	0	1	0	0	0	0	0
Apomyrma	Amblyoponinae	0	0	1	0	0	0	0	0
Apterostigma	Myrmicinae	0	1	0	0	0	0	0	0
Aptinoma	Dolichoderinae	0	0	0	1	0	0	0	0
Arnoldius	Dolichoderinae	0	0	0	0	1	1	1	0
Asphinctanilloides	Leptanilloidinae	0	1	0	0	0	0	0	0
Asphinctopone	Ponerinae	0	0	1	0	0	0	0	0
Atopomyrmex	Myrmicinae	0	0	1	0	0	0	0	0
Atta	Myrmicinae	1	1	0	0	0	0	0	0
Aulacopone	Heteroponerinae	0	0	0	0	1	0	0	0
Axinidris	Dolichoderinae	0	0	1	0	0	0	0	0
Azteca	Dolichoderinae	0	1	0	0	0	0	0	0
Bajcaridris	Formicinae	0	0	0	0	1	0	0	0
Bannapone	Amblyoponinae	0	0	0	0	0	1	0	0
Baracidris	Myrmicinae	0	0	1	0	0	0	0	0

Bariamyrma	Myrmicinae	0	1	0	0	0	0	0	0
Basiceros	Myrmicinae	0	1	0	0	0	0	0	0
Belonopelta	Ponerinae	0	1	0	0	0	0	0	0
Blepharidatta	Myrmicinae	0	1	0	0	0	0	0	0
Boloponera	Ponerinae	0	0	1	0	0	0	0	0
Bondroitia	Myrmicinae	0	0	1	0	0	0	0	0
Bothriomyrmex	Dolichoderinae	0	1	0	0	1	1	0	0
Brachymyrmex	Formicinae	1	1	0	[1]	1	0	0	[1]
Bregmatomyrma	Formicinae	0	0	0	0	0	1	0	0
Calomyrmex	Formicinae	0	0	0	0	0	0	1	0
Calyptomyrmex	Myrmicinae	0	0	1	1	0	1	1	1
Camponotus	Formicinae	1	1	1	1	1	1	1	1
Cardiocondyla	Myrmicinae	1	1	1	1	1	1	1	1
Carebara	Myrmicinae	1	1	1	1	1	1	1	1
Carebarella	Myrmicinae	0	1	0	0	0	0	0	0
Cataglyphis	Formicinae	0	0	1	0	1	1	0	0
Cataulacus	Myrmicinae	0	0	1	1	0	1	1	0
Centromyrmex	Ponerinae	0	1	1	0	0	1	0	0
Cephalotes	Myrmicinae	1	1	0	0	0	0	0	0
Cerapachys	Cerapachyinae	1	1	1	1	1	1	1	1
Chalepoxenus	Myrmicinae	0	0	0	0	1	1	0	0
Cheliomyrmex	Ecitoninae	0	1	0	0	0	0	0	0
Chimaeridris	Myrmicinae	0	0	0	0	0	1	1	0
Chronoxenus	Dolichoderinae	0	0	0	0	0	1	0	0
Cladomyrma	Formicinae	0	0	0	0	0	1	0	0
Colobostruma	Myrmicinae	0	0	0	0	0	0	1	0
Concoctio	Amblyoponinae	0	0	1	0	0	0	0	0
Condylodon	Incertae sedis	0	1	0	0	0	0	0	0
Crematogaster	Myrmicinae	1	1	1	1	1	1	1	1
Cryptomyrmex	Myrmicinae	0	1	0	0	0	0	0	0
Cryptopone	Ponerinae	1	1	1	0	1	1	1	1
Cylindromyrmex	Cerapachyinae	0	1	0	0	0	0	0	0
Cyphoidris	Myrmicinae	0	0	1	0	0	0	0	0
Cyphomyrmex	Myrmicinae	1	1	0	0	0	0	0	0
Dacatria	Myrmicinae	0	0	0	0	1	1	0	0
Dacetinops	Myrmicinae	0	0	0	0	0	1	1	0
Daceton	Myrmicinae	0	1	0	0	0	0	0	0
Decamorium	Myrmicinae	0	0	1	0	0	0	0	0
Diacamma	Ponerinae	0	0	0	0	0	1	1	0
Dicroaspis	Myrmicinae	0	0	1	0	0	0	0	0
Dilobocondyla	Myrmicinae	0	0	0	0	0	1	1	0
Dinoponera	Ponerinae	0	1	0	0	0	0	0	0
Diplomorium	Myrmicinae	0	0	1	0	0	0	0	0
Discothyrea	Proceratiinae	1	1	1	1	1	1	1	1
Doleromyrma	Dolichoderinae	0	0	0	0	0	0	1	0
Dolichoderus	Dolichoderinae	1	1	0	0	1	1	1	0
Dolioponera	Ponerinae	0	0	1	0	0	0	0	0
Dolopomyrmex	Myrmicinae	1	0	0	0	0	0	0	0
Dorylus	Dorylinae	0	0	1	0	0	1	1	0
Dorymyrmex	Dolichoderinae	1	1	0	0	0	0	0	0
Echinopla	Formicinae	0	0	0	0	0	1	1	0

continued

Genus	Subfamily	NEA	NEO	AFR	MAL	PAL	IND	AUS	OCE
Eciton	Ecitoninae	0	1	0	0	0	0	0	0
Ecphorella	Dolichoderinae	0	0	1	0	0	0	0	0
Ectatomma	Ectatomminae	0	1	0	0	0	0	0	0
Emeryopone	Ponerinae	0	0	0	0	1	1	0	0
Epopostruma	Myrmicinae	0	0	0	0	0	0	1	0
Euprenolepis	Formicinae	0	1	0	0	0	1	1	0
Eurhopalothrix	Myrmicinae	1	1	0	0	0	1	1	1
Eutetramorium	Myrmicinae	0	0	0	1	0	0	0	0
Feroponera	Ponerinae	0	0	1	0	0	0	0	0
Forelius	Dolichoderinae	1	1	0	0	0	0	0	0
Forelophilus	Formicinae	0	0	0	0	0	1	0	0
Formica	Formicinae	1	1	0	0	1	1	0	0
Formicoxenus	Myrmicinae	1	1	0	0	1	0	0	0
Froggattella	Dolichoderinae	0	0	0	0	0	0	1	0
Gauromyrmex	Myrmicinae	0	0	0	0	0	1	0	1
Gesomyrmex	Formicinae	0	0	0	0	0	1	0	0
Gigantiops	Formicinae	0	1	0	0	0	0	0	0
Gnamptogenys	Ectatomminae	1	1	0	0	1	1	1	1
Goniomma	Myrmicinae	0	0	0	0	1	0	0	0
Gracilidris	Dolichoderinae	0	1	0	0	0	0	0	0
Harpagoxenus	Myrmicinae	1	0	0	0	1	0	0	0
Harpegnathos	Ponerinae	0	0	0	0	0	1	0	0
Heteroponera	Heteroponerinae	0	1	0	0	0	0	1	0
Huberia	Myrmicinae	0	0	0	0	0	0	1	0
Hylomyrma	Myrmicinae	0	1	0	0	0	0	0	0
Hypoponera	Ponerinae	1	1	1	1	1	1	1	1
Indomyrma	Myrmicinae	0	0	0	0	0	1	0	0
Iridomyrmex	Dolichoderinae	0	0	0	0	1	1	1	1
Ishakidris	Myrmicinae	0	0	0	0	0	1	0	0
Kartidris	Myrmicinae	0	0	0	0	0	1	0	0
Labidus	Ecitoninae	1	1	0	0	0	0	0	0
Lachnomyrmex	Myrmicinae	0	1	0	0	0	0	0	0
Lasiomyrma	Myrmicinae	0	0	0	0	0	1	0	0
Lasiophanes	Formicinae	0	1	0	0	0	0	0	0
Lasius	Formicinae	1	1	0	0	1	1	0	0
Lenomyrmex	Myrmicinae	0	1	0	0	0	0	0	0
Lepisiota	Formicinae	0	0	1	1	1	1	0	1
Leptanilla	Leptanillinae	0	0	1	0	1	1	1	0
Leptanilloides	Leptanilloidinae	0	1	0	0	0	0	0	0
Leptogenys	Ponerinae	1	1	1	1	1	1	1	1
Leptomyrmex	Dolichoderinae	0	0	0	0	0	0	1	0
Leptothorax	Myrmicinae	1	1	1	1	1	1	0	0
Linepithema	Dolichoderinae	1	1	0	0	[1]	[1]	[1]	[1]
Liometopum	Dolichoderinae	1	1	0	0	1	1	0	0
Liomyrmex	Myrmicinae	0	0	0	0	0	1	1	0
Loboponera	Ponerinae	0	0	1	0	0	0	0	0
Lophomyrmex	Myrmicinae	0	0	0	0	0	1	0	0
Lordomyrma	Myrmicinae	0	0	0	0	1	1	1	1
Loweriella	Dolichoderinae	0	0	0	0	0	1	0	0
Machomyrma	Myrmicinae	0	0	0	0	0	0	1	0

Manica	Myrmicinae	1	0	0	0	1	0	0	0
Martialis	Martialinae	0	1	0	0	0	0	0	0
Mayriella	Myrmicinae	0	0	0	0	0	1	1	0
Megalomyrmex	Myrmicinae	0	1	0	0	0	0	0	0
Melissotarsus	Myrmicinae	0	0	1	1	0	0	0	0
Melophorus	Formicinae	0	0	0	0	0	0	1	0
Meranoplus	Myrmicinae	0	0	1	1	0	1	1	0
Mesostruma	Myrmicinae	0	0	0	0	0	0	1	0
Messor	Myrmicinae	1	1	1	0	1	1	0	0
Metapone	Myrmicinae	0	0	1	1	0	1	1	1
Microdaceton	Myrmicinae	0	0	1	0	0	0	0	0
Monomorium	Myrmicinae	1	1	1	1	1	1	1	1
Mycetagroicus	Myrmicinae	0	1	0	0	0	0	0	0
Mycetarotes	Myrmicinae	0	1	0	0	0	0	0	0
Mycetophylax	Myrmicinae	0	1	0	0	0	0	0	0
Mycetosoritis	Myrmicinae	1	1	0	0	0	0	0	0
Mycocepurus	Myrmicinae	0	1	0	0	0	0	0	0
Myopias	Ponerinae	0	0	0	0	0	1	1	0
Myopopone	Amblyoponinae	0	0	0	0	0	1	1	0
Myrcidris	Pseudomyrmecinae	0	1	0	0	0	0	0	0
Myrmecia	Myrmeciinae	0	0	0	0	0	0	1	0
Myrmecina	Myrmicinae	1	1	0	0	1	1	1	1
Myrmecocystus	Formicinae	1	1	0	0	0	0	0	0
Myrmecorhynchus	Formicinae	0	0	0	0	0	0	1	0
Myrmelachista	Formicinae	0	1	0	0	0	0	0	0
Myrmica	Myrmicinae	1	1	0	0	1	1	0	0
Myrmicaria	Myrmicinae	0	0	1	0	0	1	0	0
Myrmicocrypta	Myrmicinae	0	1	0	0	0	0	0	0
Myrmoteras	Formicinae	0	0	0	0	0	1	1	0
Myrmoxenus	Myrmicinae	0	0	0	0	1	0	0	0
Mystrium	Amblyoponinae	0	0	1	1	0	1	1	0
Nebothriomyrmex	Dolichoderinae	0	0	0	0	0	0	1	0
Neivamyrmex	Ecitoninae	1	1	0	0	0	0	0	0
Nesomyrmex	Myrmicinae	1	1	1	1	0	1	0	0
Nomamyrmex	Ecitoninae	1	1	0	0	0	0	0	0
Noonilla	Incertae sedis	0	0	0	0	0	1	0	0
Nothomyrmecia	Myrmeciinae	0	0	0	0	0	0	1	0
Notoncus	Formicinae	0	0	0	0	0	0	1	0
Notostigma	Formicinae	0	0	0	0	0	0	1	0
Ochetellus	Dolichoderinae	1	0	0	[1]	1	1	1	1
Ochetomyrmex	Myrmicinae	0	1	0	0	0	0	0	0
Octostruma	Myrmicinae	0	1	0	0	0	0	0	0
Ocymyrmex	Myrmicinae	0	0	1	0	0	0	0	0
Odontomachus	Ponerinae	1	1	1	1	1	1	1	1
Odontoponera	Ponerinae	0	0	0	0	1	1	0	0
Oecophylla	Formicinae	0	0	1	0	0	1	1	0
Onychomyrmex	Amblyoponinae	0	0	0	0	0	0	1	0
Opamyrma	Amblyoponinae	0	0	0	0	0	1	0	0
Opisthopsis	Formicinae	0	0	0	0	0	0	1	0
Orectognathus	Myrmicinae	0	0	0	0	0	0	1	0
Overbeckia	Formicinae	0	0	0	0	0	1	0	0

continued

Genus	Subfamily	NEA	NEO	AFR	MAL	PAL	IND	AUS	OCE
Oxyepoecus	Myrmicinae	0	1	0	0	0	0	0	0
Oxyopomyrmex	Myrmicinae	0	0	0	0	1	0	0	0
Pachycondyla	Ponerinae	1	1	1	1	1	1	1	1
Papyrius	Dolichoderinae	0	0	0	0	0	0	1	0
Paraponera	Paraponerinae	0	1	0	0	0	0	0	0
Paraprionopelta	Amblyoponinae	0	1	0	0	0	0	0	0
Paratopula	Myrmicinae	0	0	0	0	0	1	1	0
Paratrechina	Formicinae	1	1	1	1	1	1	1	1
Parvimyrma	Myrmicinae	0	0	0	0	0	1	0	0
Perissomyrmex	Myrmicinae	0	1	0	0	1	1	0	0
Peronomyrmex	Myrmicinae	0	0	0	0	0	0	1	0
Petalomyrmex	Formicinae	0	0	1	0	0	0	0	0
Phalacromyrmex	Myrmicinae	0	1	0	0	0	0	0	0
Phasmomyrmex	Formicinae	0	0	1	0	0	0	0	0
Phaulomyrma	Leptanillinae	0	0	0	0	0	1	0	0
Pheidole	Myrmicinae	1	1	1	1	1	1	1	1
Pheidologeton	Myrmicinae	0	0	1	0	1	1	1	0
Philidris	Dolichoderinae	0	0	0	0	0	1	1	1
Phrynoponera	Ponerinae	0	0	1	0	0	0	0	0
Pilotrochus	Myrmicinae	0	0	0	1	0	0	0	0
Plagiolepis	Formicinae	1	1	1	1	1	1	1	[1]
Platythyrea	Ponerinae	1	1	1	1	0	1	1	[1]
Plectroctena	Ponerinae	0	0	1	0	0	0	0	0
Podomyrma	Myrmicinae	0	0	0	0	0	1	1	0
Poecilomyrma	Myrmicinae	0	0	0	0	0	0	0	1
Pogonomyrmex	Myrmicinae	1	1	0	0	0	0	0	0
Polyergus	Formicinae	1	1	0	0	1	0	0	0
Polyrhachis	Formicinae	0	0	1	0	1	1	1	1
Ponera	Ponerinae	1	1	1	[1]	1	1	1	1
Prenolepis	Formicinae	1	1	0	0	1	1	1	0
Prionopelta	Amblyoponinae	1	1	1	1	0	1	1	1
Pristomyrmex	Myrmicinae	0	0	1	1	1	1	1	1
Proatta	Myrmicinae	0	0	0	0	0	1	0	0
Probolomyrmex	Proceratiinae	0	1	1	0	1	1	1	0
Proceratium	Proceratiinae	1	1	1	1	1	1	1	1
Procryptocerus	Myrmicinae	0	1	0	0	0	0	0	0
Proformica	Formicinae	0	0	0	0	1	0	0	0
Prolasius	Formicinae	0	0	0	0	0	0	1	0
Promyopias	Ponerinae	0	0	1	0	0	0	0	0
Protalaridris	Myrmicinae	0	1	0	0	0	0	0	0
Protanilla	Leptanillinae	0	0	0	0	1	1	0	0
Protomognathus	Myrmicinae	1	0	0	0	0	0	0	0
Psalidomyrmex	Ponerinae	0	0	1	0	0	0	0	0
Pseudoatta	Myrmicinae	0	1	0	0	0	0	0	0
Pseudolasius	Formicinae	0	0	1	1	1	1	1	0
Pseudomyrmex	Pseudomyrmecinae	1	1	0	0	0	0	0	[1]
Pseudonotoncus	Formicinae	0	0	0	0	0	0	1	0
Pyramica	Myrmicinae	1	1	1	1	1	1	1	1
Ravavy	Dolichoderinae	0	0	0	1	0	0	0	0
Recurvidris	Myrmicinae	0	0	0	0	1	1	1	0

Rhopalomastix	Myrmicinae	0	0	0	0	0	1	1	0
Rhopalothrix	Myrmicinae	0	1	0	0	0	0	1	0
Rhoptromyrmex	Myrmicinae	0	0	1	0	1	1	1	0
Rhytidoponera	Ectatomminae	0	0	0	0	0	0	1	0
Rogeria	Myrmicinae	1	1	0	0	0	0	1	1
Romblonella	Myrmicinae	0	0	0	0	0	1	1	1
Rossomyrmex	Formicinae	0	0	0	0	1	0	0	0
Rostromyrmex	Myrmicinae	0	0	0	0	0	1	0	0
Rotastruma	Myrmicinae	0	0	0	0	0	1	0	0
Santschiella	Formicinae	0	0	1	0	0	0	0	0
Secostruma	Myrmicinae	0	0	0	0	0	1	1	0
Sericomyrmex	Myrmicinae	0	1	0	0	0	0	0	0
Simopelta	Ponerinae	0	1	0	0	0	0	0	0
Simopone	Cerapachyinae	0	0	1	1	0	1	1	0
Solenopsis	Myrmicinae	1	1	1	1	1	1	1	1
Sphinctomyrmex	Cerapachyinae	0	1	1	0	0	1	1	0
Stegomyrmex	Myrmicinae	0	1	0	0	0	0	0	0
Stenamma	Myrmicinae	1	1	0	0	1	1	0	0
Stereomyrmex	Myrmicinae	0	0	0	0	0	1	1	0
Stigmacros	Formicinae	0	0	0	0	0	0	1	0
Streblognathus	Ponerinae	0	0	1	0	0	0	0	0
Strongylognathus	Myrmicinae	0	0	0	0	1	0	0	0
Strumigenys	Myrmicinae	1	1	1	1	1	1	1	1
Talaridris	Myrmicinae	0	1	0	0	0	0	0	0
Tapinolepis	Formicinae	0	0	1	0	0	0	0	0
Tapinoma	Dolichoderinae	1	1	1	1	1	1	1	1
Tatuidris	Agroecomyrmecinae	0	1	0	0	0	0	0	0
Technomyrmex	Dolichoderinae	1	1	1	1	1	1	1	1
Teleutomyrmex	Myrmicinae	0	0	0	0	1	0	0	0
Temnothorax	Myrmicinae	1	1	1	1	1	1	0	0
Terataner	Myrmicinae	0	0	1	1	0	0	0	0
Teratomyrmex	Formicinae	0	0	0	0	0	0	1	0
Tetheamyrma	Myrmicinae	0	0	0	0	0	1	0	0
Tetramorium	Myrmicinae	1	1	1	1	1	1	1	1
Tetraponera	Pseudomyrmecinae	0	0	1	1	1	1	1	0
Thaumatomyrmex	Ponerinae	0	1	0	0	0	0	0	0
Trachymyrmex	Myrmicinae	1	1	0	0	0	0	0	0
Tranopelta	Myrmicinae	0	1	0	0	0	0	0	0
Turneria	Dolichoderinae	0	0	0	0	0	0	1	0
Typhlomyrmex	Ectatomminae	1	1	0	0	0	0	0	0
Tyrannomyrmex	Myrmicinae	0	0	0	0	0	1	0	0
Vollenhovia	Myrmicinae	1	0	0	0	1	1	1	1
Vombisidris	Myrmicinae	0	0	0	0	0	1	1	0
Wasmannia	Myrmicinae	1	1	0	0	0	0	1	[1]
Xenomyrmex	Myrmicinae	1	1	0	0	0	1	0	0
Yavnella	Leptanillinae	0	0	0	0	1	1	0	0
	total	73	128	88	47	82	128	115	44
	endemic	2	52	31	5	10	24	30	1