# 1 · *Introducing wood ants: evolution, phylogeny, identification and distribution*

JENNI A. STOCKAN, ELVA J. H. ROBINSON, JAMES C. TRAGER, IZUMI YAO AND BERNHARD SEIFERT

Few insects in the cool temperate northern hemisphere are as conspicuous as red wood ants. Most red wood ants build large and enduring nest mounds reaching more than 2 m in height, penetrating considerably further beneath the ground surface and thatched on top with a layer of plant material. These mounds are marvels of engineering with a complex array of tunnels and chambers in a carefully controlled environment. Nests may be interlinked, forming, in extreme cases, vast colonies of up to 400 million individual ants covering an area of more than 2.5 $km^2$. Their sheer abundance and collective biomass in temperate forests can rival any mammalian predator.

Red wood ants properly belong to the subgenus *Formica sensu stricto* or *F. rufa* group, and can also be commonly referred to as true wood ants, thatch ants or mound ants (hereafter 'wood ants'). These names derive from the habitat, nesting habit and colour of the adults, which are bicoloured red and brownish-black. Contained within this group of ants are several morphologically and ecologically similar species distributed throughout the Holarctic.

More impressive perhaps than even their numerical dominance is their ecological significance in driving ecosystem processes and function both above and below ground. With a role in predator–prey dynamics, nutrient cycling, seed dispersion, habitat provision and modification, and plant and tree growth, wood ants can truly be described as keystone species. As a result of their ecological importance, wood ants are protected by law in some countries, yet their populations remain threatened from a

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variety of sources, not least, loss of suitable habitat. This chapter describes species that are currently considered members of the subgenus *Formica sensu stricto*; their evolution, identification, habitat and distribution. The concept of red wood ants as social insects is introduced. The rest of the book will cover reproductive biology and social systems (Chapter 2), population genetics (Chapter 3) and ecology (Chapter 4), colony and species recognition (Chapter 5), interspecific competition (Chapter 6), foraging and interactions with other organisms (Chapters 7 and 8), nutrient cycling (Chapter 9), similarities and differences between North American and Eurasian wood ants (Chapter 10), monitoring and conservation (Chapters 11 and 12) and future research questions (Chapter 13).

## Evolution and phylogeny

Diversification of ants (Hymenoptera, Formicidae) began in the early Cretaceous, 115–135 million years before present (MYBP), the subfamily Formicinae appearing around 92 MYBP (Grimaldi and Agosti 2000). Studies on mitochondrial (mt) DNA from across Europe suggest that the *F. rufa* group separated from other *Formica* species around 15 MYBP (Goropashnaya *et al.* 2004b). Radiation into at least eight Eurasian species probably took place before the end of the Pleistocene (Goropashnaya *et al.* 2004a; Figure 1.1). Hybridisation and subsequent isolation is likely to have produced further species (Nonacs 2006) and may continue to do so; a surprisingly high proportion (*c.* 60%) of Eurasian species retain the ability to produce fertile hybrids (Seifert and Goropashnaya 2004; Korczyńska *et al.* 2010). The social organisation of species characterised by highly polygynous societies with large colonial networks, such as *F. aquilonia*, could be another driving factor promoting speciation (Gyllenstrand 2002). In these wood ant societies, female (and male) dispersal is very often limited and populations can therefore become isolated over time.

Phylogenetic relationships have been constructed for some, but not all, of the Eurasian species, and care is urged in the interpretation of these (Seifert and Goropashnaya 2004). At the root of the phylogenetic tree of Eurasian species is the species which gives its name to the species group, *F. rufa,* together with the closely related *F. polyctena* (Goropashnaya *et al.* 2012; Figure 1.1). This implies recent divergence and incomplete lineage sorting between them (Goropashnaya *et al.* 2004a). The lack of hiatus in the mtDNA phylogeny, e.g. the mtDNA sequences of these species differ by only 1.3% (Kulmuni *et al.* 2010), is consistent with the occurrence of frequent hybridisation between *F. rufa* and *F. polyctena* in nature (Seifert

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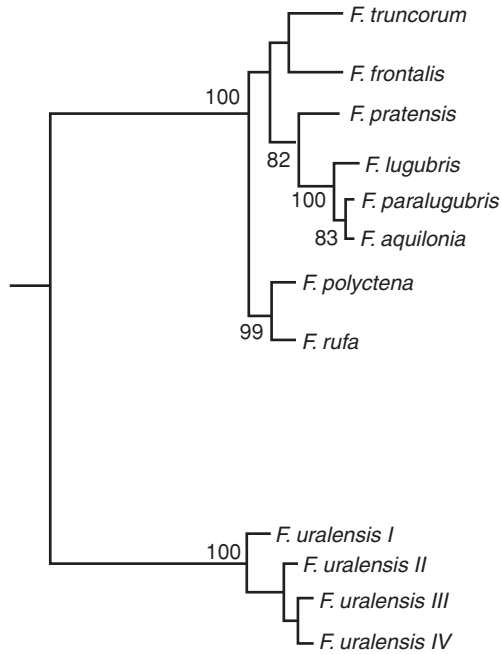



*Figure 1.1* Phylogenetic cladogram of Eurasian wood ant species based on mitochondrial cytochrome *b* sequences (redrawn with permission from Goropashnaya *et al.* 2012).

1991; Czechowski 1996). The *F. rufa/polyctena* clade is believed to have separated from other wood ant species around 490 thousand years before present (TYBP) with the split between *F. aquilonia* and *F. lugubris*, taking place around 100 TYBP (Goropashnaya *et al.* 2003). The *F. pratensis* branch separated around 350 TYBP (Goropashnaya *et al.* 2004b) and is thought to be distinct from all the other core species (Goropashnaya *et al.* 2004a; Bernasconi *et al.* 2011). However, mtDNA evidence suggests a closer association with *F. aquilonia, F. paralugubris* and *F. lugubris* (Pamilo *et al.* 1979; Goropashnaya *et al.* 2004a; Figure 1.1) than any other members of the group. The clade of *F. truncorum* and *F. frontalis* forms a third clade. *Formica uralensis* follows a completely separate phylogenetic lineage, and many have suggested it should be recategorised as a new subgenus (Goropashnaya *et al.* 2012). The phylogeny of North American wood ants is currently unknown but these species are believed to represent an older monophyletic lineage, which is a sister group to the Eurasian *F. rufa* group (see Chapter 10).

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*Figure 1.2* A typical wood ant (*Formica aquilonia*) showing the body form. For colouring, see front cover (photo by G. Pozsgai, reproduced with permission).

## Species identification

Accurate identification of wood ants has been a long-standing problem, yet remains a fundamental prerequisite for any study of ecology and conservation (Figure 1.2). The taxonomic instability of the subgenus resulting from morphological similarity, high intraspecific variability and the ability of some species to hybridise (Seifert 1999; Seifert and Goropashnaya 2004) or form mixed colonies (Seifert 1991; Czechowski 1996; Seifert *et al.* 2010) has led to much debate, but also much neglect. The species set considered members of the *F. rufa* group (Table 1.1) is likely to change still further with new and developing chemical and molecular methods such as alarm (Cherix 1983) and sex pheromones (Walter *et al.* 1993), behavioural tests such as brood recognition (Rosengren and Cherix 1981; Rosengren *et al.* 1994), chemical analysis of cuticular hydrocarbons (Martin *et al.* 2008), allozymes (Pamilo *et al.* 1992), mtDNA (Goropashnaya *et al.* 2004a, 2012) and microsatellites (i.e. nuclear DNA) (Gyllenstrand *et al.* 2004; Bernasconi *et al.* 2010, 2011) as molecular markers. Without question is the inclusion in the *F. rufa* group of the six 'core' species known as the *rufa* complex (*rufa*, *aquilonia*, *lugubris*, *paralugubris*, *polyctena* and *pratensis*) together with *F. truncorum* and its Asian and Iberian close relatives, the *truncorum* complex. These two complexes, though apparently not forming distinct phylogenetic groupings, exhibit morphological and ecological differences (e.g. nest populations of the *F. truncorum* complex are smaller (Mabelis and Korczyńska 2001)). More debatable is *F. uralensis*, which although ecologically similar to other species within the group, founding nests through temporary social parasitism and building nest mounds, is phylogenetically distinct. Furthermore, there are as yet

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Table 1.1 *Species currently considered members of the subgenus* Formica s. str. *group.*

| Palearctic species | Nearctic species |
|---|---|
| [a]*Formica rufa* Linnaeus 1761 | *Formica calviceps* Cole 1954 |
| *Formica dusmeti* Emery 1909 | *Formica ciliata* Mayr 1886 |
| [a]*Formica aquilonia* Yarrow 1955 | *Formica coloradensis* Creighton 1940 |
| [a]*Formica lugubris* Zetterstedt 1838 | *Formica comata* Wheeler 1909 |
| *Formica paralugubris* Seifert 1996 | *Formica criniventris* Wheeler 1912 |
| [a]*Formica polyctena* Förster 1850 | *Formica ferocula* Wheeler 1913 |
| [a]*Formica pratensis* Retzius 1783 | *Formica fossaceps* Buren 1942 |
| *Formica truncorum* Fabricius 1804 | *Formica integra* Nylander 1856 |
| *Formica sinensis* Wheeler 1913 | *Formica integroides* Emery 1913 |
| *Formica frontalis* Santschi 1909 | *Formica laeviceps* Creighton 1940 |
| *Formica yessensis* Forel 1901 | *Formica mucescens* Wheeler 1913 |
| [a]*Formica uralensis* Ruzsky 1895 | *Formica obscuripes* Forel 1886 |
| *Formica opaca* Nylander 1856 | *Formica obscuriventris* Mayr 1970 |
| | *Formica oreas* Wheeler 1903 |
| | [b]*Formica planipilis* Creighton 1940 |
| | [c]*Formica prociliata* Kennedy and Dennis 1937 |
| | *Formica propinqua* Creighton 1940 |
| | *Formica ravida* Creighton 1940 |
| | *Formica subnitens* Creighton 1940 |

[a] Species appearing on the International Union for Conservation of Nature (IUCN) red list of threatened species.
[b] May be a synonym of *F. obscuripes*.
[c] May be a junior synonym of *F. ferocula*.

undescribed species (Bernasconi *et al*. 2011; B. Seifert, personal observation, 2014). Species previously attributed to the North American *microgyna* group are now considered part of the *F. rufa* group by some experts at least (Wheeler and Wheeler 1986; see Chapter 10).

Morphology remains the best method of species discrimination but is time consuming and requires much experience. The identification keys provided here are divided into Palearctic and Nearctic species and are based on the external morphology of workers and using multiple discriminant features including characters such as body part measurements, number of setae and hair length.

## Key to Palaearctic species in the *Formica rufa* group

This key does not include undescribed species and considers only one interspecific hybrid. Unilateral setae numbers are means of both sides.

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All seta counts refer only to setae protruding more than 10 μm from the cuticular surface (also known as 'standing' setae). Due to the enormous intraspecific character variation in critical species groups, nest sample means of 3–10 workers should be considered. The data refer to workers with a cephalic head size (CS) of 1.5–2.0 mm. Species groups not belonging to the *F. rufa* group are keyed to the subgenus level only.

**Character definitions**

**CL** – maximum cephalic length in median line; the head must be carefully tilted to the position with the true maximum. Excavations of occiput and/or clypeus reduce CL.

**CW** – maximum cephalic width.

**CS** – mean of CL and CW.

**CUHL** – length of longest hair on underside of head (not mean of both sides!).

**EyeHL** – the length of the longest hair on the eyes including minute hairs visible at magnifications ≥ × 150. In case of curved hairs measure the chord length.

**MetHL** – length of the longest seta on a metapleuro-propodeal surface. This is below a straight reference line that is directed parallel to the straight section of the lower metapleural margin and touches the lower margin of propodeal spiracle. The area of caudal propodeal slope below this line is included but weir hairs at the orifice of the metapleural gland and setae near to the petiolar junction are excluded. Care should be taken to visualise the lateral suture between the meso- and metapleuron; i.e. mean of both sides.

**mPnHL** – mean pronotal hair length. Applied measuring schedule: select one of the longest hairs on dorsal pronotum and calculate the arithmetic mean length of this hair and of its six nearest neighbours. Proprioreceptive setae on anterior pronotal shield are excluded.

**nCH** – unilateral number of standing setae protruding more than 10 μm from head silhouette as seen in full face view. Counting should begin at the level of anterior eye margin and end at the median occiput. A full depth of focus should be used for counting and the parallax error considered.

**nCU** – unilateral number of standing setae on the underside of the head, as visible in lateral view.

**nMet** – unilateral setae number on the metapleuro-propodeal area (see under MetHL).

**nPn** – unilateral setae number on pronotum.

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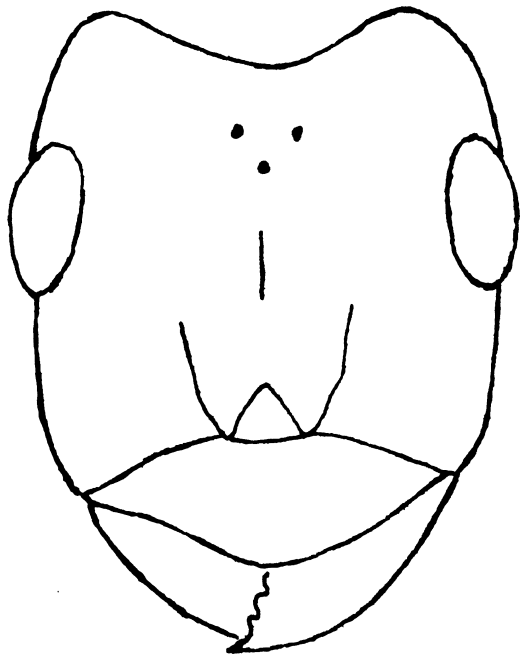


*Figure: 1.3* Head of a *Coptoformica* worker showing the clearly excavated posterior margin of the head.

**nSc** – unilateral setae number on dorsal plane of scape.
**SL** – maximum scape length, excluding articulary condyle and its neck.
**SMAX** – maximum scape width at midpoint; data of both scapes should be averaged.

**1a** Posterior margin of head clearly excavated and with pronounced occipital corners (Figure 1.3); with maximum median head length in focal plane, depth of excavation 4.9–9.6% of CW. Posterior (basal) edge of mandibles near to the cutting edge with 1–3 accessory denticles. . . . . **Subgenus *Coptoformica***
**1b** Posterior margin of head convex, straight or only weakly excavated. Lateral occiput without pronounced corners (Figures 1.4 and 1.5). Posterior edge of mandible without denticles . . . . . **2**
**2a** Anteromedian clypeal margin clearly emarginate (Figure 1.5) . . . . . **Subgenus *Raptiformica***
**2b** Anteromedian clypeal margin not emarginate (Figure 1.4) . . . . . **3**
**3a** Frontal triangle significantly more shining than adjacent surfaces. . . . . **Subgenus *Formica* s.str 5**

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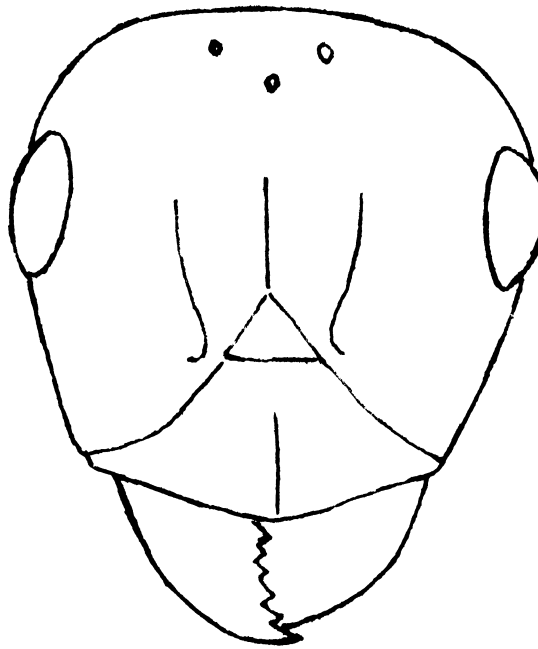


*Figure 1.4* Head of a worker with a straight posterior margin of the head.

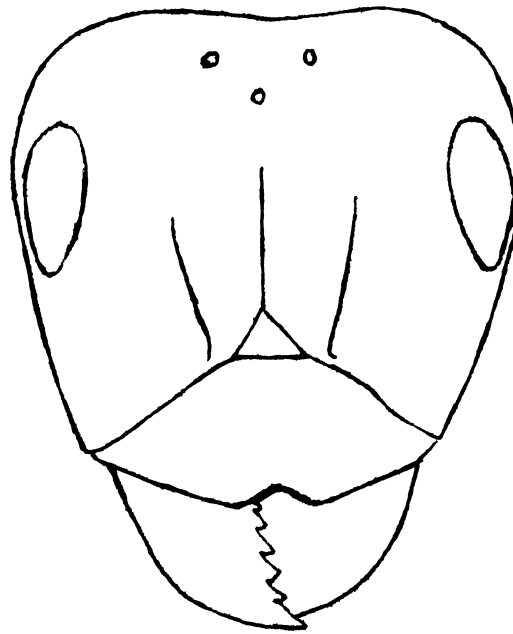


*Figure 1.5 Raptiformica* worker head showing only weakly excavated posterior margin and emarginated clypeus.

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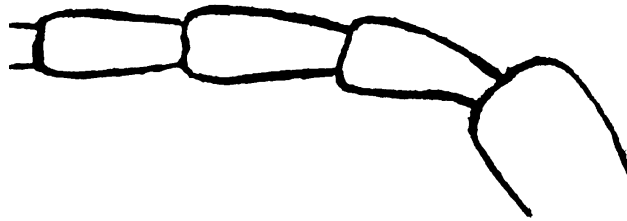


*Figure 1.6* Funiculus of antenna showing 2nd and 3rd segments at least twice as long as wide.

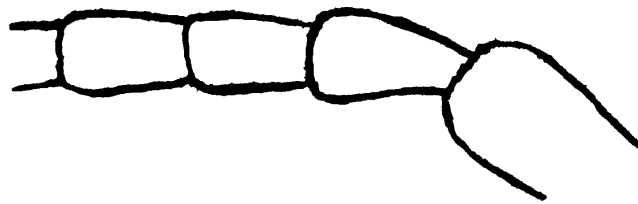


*Figure 1.7* Funiculus of antenna showing 2nd and 3rd segments less than twice as long as wide.

**3b** Reflexion properties of frontal triangle not contrasting to those of adjacent surfaces. Frontal triangle in most species matt; if shining, then whole dorsal head, mesosoma and gaster also shining ..... **4**

**4a** Scape rather short and thick, SL/CW<0.960. Pigmentation characteristic: whole head, pronotum, gaster and occasionally dorsal mesonotum blackish; remaining mesosoma reddish brown. Whole body matt, posterior margin of head and propodeum without standing setae ..... ***uralensis***

**4b** Scape long and slender, SL/CW>0.960. Pigmentation pattern deviating ..... **Subgenus *Serviformica***

**5a** 2nd and 3rd funiculus segments at least twice as long as wide (Figure 1.6). Middle part of lateral clypeus more deeply depressed than in *F. rufa*. Typical pigmentation in medium-sized to large workers: whole head, mesosoma and petiole light reddish brown (specimens with pigmentation reminiscent of *F. rufa* are rare), *Formica truncorum* complex. All following numeric data are nest means ..... **6**

**5b** 2nd and 3rd funiculus segments less than twice as long as wide (Figure 1.7). Middle part of lateral clypeus less deeply depressed

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(*F. rufa* may serve as standard for group 5b; however, the *hind portion* of lateral clypeus may be as deeply depressed as in *truncorum*!). Dorsal vertex almost always with blackish pigmentation. All following numeric data are nest means ..... **9**

**6a** Posterior head without standing setae, whole surface of mesosoma without or only very few, short setae, underside of head with few setae, nCU<7, Iberia only ..... ***dusmeti***

**6b** Posterior head with standing setae, whole surface of mesosoma with numerous setae, underside of head with many setae, nCU>7 ..... **7**

**7a** Iberia, Tibet to NE China and N Japan. Dorsal plane of scape without or only occasional short setae, nSc 0–3 ..... **8**

**7b** Other regions: temperate to boreo-montane zone of Palaearctic from 5°E to 143°E. Dorsal plane of scape usually with several to many standing setae, nSc 2–27. Sympatric with *yessensis* in Hokkaido, differs here from the latter by more developed pilosity on dorsum of scape and underside of head (nSC>2, nCU >30). Sympatric with *sinensis* in NE China, differs here from the latter by longer hairs on eyes (EyeHL> 15 μm) and more profuse pilosity on hind margin of head (nCH>25) ..... ***truncorum***

**8a** Tibet to NE China. Eyes without or with minute hairs, EyeHL 0–15 μm. Underside of head with profuse setae, nCU 13–39 ..... ***sinensis***

**8b** North Japan. Eyes with significantly longer hairs, EyeHL 10–35 μm. Underside of head with less profuse setae, nCU 9–27 ..... ***yessensis***

**8c** Iberia. Eyes with significantly longer hairs, EyeHL 1–35 μm. Underside of head with less profuse setae, nCU 9–27 ..... ***frontalis***

**9a** With maximum median CL in focal plane, posterior contour of head hairless. In very hairy *F. rufa*, nCH occasionally reaching 3.6, with 15–60 μm long hairs, but then nPn >20 and SL/SMAX 10.13 ± 0.29 ..... **10**

**9b** With maximum median CL in focal plane, contour of head from median occiput to anterior eye margin with >3 setae. In weakly haired *F. aquilonia,* nCH occasionally falling to 1.3, but then nPn <13 and SL/SMAX 9.28 ± 0.23 ..... **11**

**10a** Weakly haired: nCU 0.1–3.0, CUHL 7–97 μm, nPN 0.1–5.6, mPnHL 6–55 μm, nPR 0–5.2, nCH 0–0.9 (setae minute). Scape rather slender: SL/SMAX 10.00 ± 0.24 ..... ***polyctena***

**10b** Moderately hairy: nCU 1.9–6.6, CUHL 96–197 μm, nPN 5.8–16.0, mPNHL 47–83 μm, nPR 4.4–11.2, nCH 0–1.2 (setae minute). Scape rather slender: SL/SMAX 10.00 ± 0.24 ... ***rufa* × *polyctena***

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**10c** More strongly haired: nCU 5.1–11.0, CUHL 155–224 μm. nPN 12.5–45.0, mPnHL 61–102 μm, nPR 8.5–25.1, nCH 0–3.6 (setae small). Scape rather slender: SL/SMAX 10.13 ± 0.29 ..... ***rufa***

**11a** Discriminant 0.050*nCH +0.034 MetHL −5.113<0. Longest propodeo-metapleural hair below level of propodeal spiracle shorter: MetHL 0–142 μm. With maximum median CL in focal plane, contour of head from median occiput to anterior eye margin with fewer setae: nCH 1.3–12.3 (*F. opaca* is similar in nCH but differs by much longer gular and mesosomal setae: CUHL>175 μm, mPnHL>80 μm, MetHL>175 μm). In Central Europe only in the mountains between 550 and 2100 m a.s.l. and in the Alps westwards to 9°E (reports of occurrences farther west on mainland Europe should be checked) ..... ***aquilonia***

**11b** Discriminant 0.050*nCH +0.034 MetHL −5.113>0. Longest propodeo-metapleural hair below level of propodeal spiracle longer: MetHL 134–237 μm. With maximum median CL in focal plane, contour of head from median occiput to anterior eye margin with more setae: nCH 4–65 ..... **12**

**12a** Number of setae on underside of head, sides of mesopleuron and lower propodeum metapleuron smaller: nCH 4–8, nMet 2–5. Russian Far East (Ussuria) ..... ***opaca***

**12b** Number of setae on underside of head and sides of lower propodeum/metapleuron larger: nCH 5–62, nMet 4–21 ..... **13**

**13a** Scape more compact: SL/SMAX 8.45–10.07. Frons appearing at low magnification not perfectly matt, with a mild silky shine. This overall impression is produced by a weaker microsculpture with more longitudinal and less reticulate elements, particularly along the frontal line and anterolaterally from mid-ocellus. Generally boreo-montane species. Discriminant for entire western Palaearctic [with CS in mm] −0.355 CL/CW−6.909 SL/CS+3.06 SL/SMAX−10.774 PEW/CS+0.418 CS−19.5<0 ..... **14**

**13b** Scape slender: SL/SMAX 9.94–11.74. Frons matt. This overall impression is produced by a stronger more reticulate microsculpture. More xerothermic, woodland and woodland–steppe habitats. Discriminant for entire western Palaearctic [with CS in mm] −0.355 CL/CW−6.909 SL/CS+3.06 SL/SMAX−10.774 PEW/CS+0.418 CS−19.5>0 ..... ***pratensis***

**14a** Only western Alps, ranging east to approximately 11°E. Pronotal setae shorter: mPNHL 61–93 μm. Propodeo-metapleural area below level of propodeal spiracle with fewer and shorter setae:

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nMet 3.3–9.7, MetHL 130–174 μm. Discriminant 0.068 mPNHL +0.011 MetHL +0.465 nMET +0.83 SL/SMAX +19.004 CL/CW −15.207 SL/CS 7.13 PEW/CS −0.028 nSC −0.227 nCH −14.437<0 ..... ***paralugubris***

**14b** Pronotal setae longer: mPNHL 79–127 μm. Propodeo-metapleural area below level of propodeal spiracle with more and longer setae: nMet 6.5–14.8, MetHL 153–225 μm. Discriminant 0.068 mPNHL +0.011 MetHL +0.465 nMET +0.83 SL/SMAX +19.004 CL/CW −15.207 SL/CS −7.13 PEW/CS −0.028 nSC −0.227 nCH −14.437>0 ..... ***lugubris***

## Key to Nearctic species in the *Formica rufa* group

In the following key, *Formica reflexa* and *F. dakotensis*, which are traditionally placed in the *rufa* complex, and the introduced *F. paralugubris* (Seifert 2016), have been excluded.

**1a** Erect setae of pronotum widen from base to a flattened apex broader than the shaft of the seta; major workers small, outstretched length from clypeal margin to acidopore rarely exceeding 6 mm, their head capsule in full face view usually longer than broad ..... ***microgyna* complex** (not further keyed)

**1b** Erect setae of pronotum tapering or if blunt-tipped, not broader apically nor spatulate; major workers larger, outstretched length exceeding 6 mm, often up to 8–9 mm; head capsule of largest workers in full face view most often broader than long ..... ***rufa* group *sensu stricto* 2**

**2a** Antennal scapes with <10 setae, or most often without erect or suberect setae except for a few near the distal end (Pacific Northwest *F. obscuripes* may have more, but these are very short and decumbent), when present on the shaft, setae occur singly and are scattered ... **3**

**2b** Antennal scapes with >12 setae, often many more erect setae on all surfaces, these not uncommonly appearing paired ..... ***oreas***

**3a** Cross section of median portion of clypeus box-like, dorsal surface meeting steeply descending sides through a distinct angle, dorsal view of clypeus appearing pinched in from the sides and broadly hourglass shaped; clypeal fossae deep, broad (Figure 1.8) ..... **4**

**3b** Cross section of median portion of clypeus parabolic, descending to clypeal fossae through an even curve or broadly rounded angle which begins at median carina, dorsal view of median clypeus not

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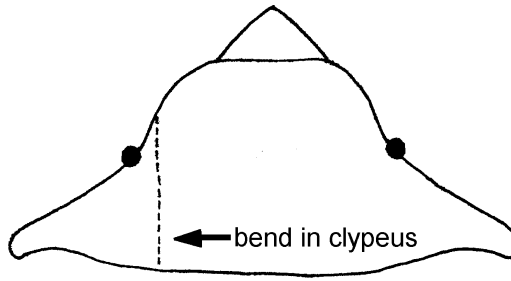



*Figure 1.8* Clypeus of a worker of *F. laeviceps*. The dashed line indicated by the arrow represents a bend in the clypeus, which makes the middle part of the clypeus protrude into a box-like or rectangular surface (adapted from Mackay and Mackay 2002).

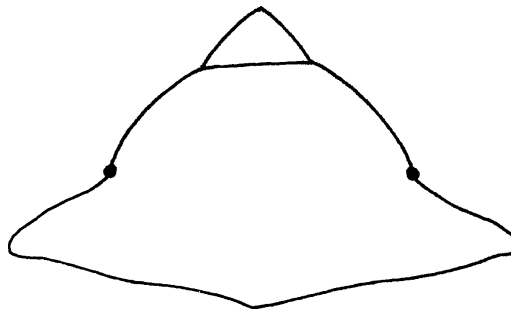


*Figure 1.9* Clypeus of a worker of *F. obscuripes* in which the clypeus is not strongly bent and the surface only weakly convex, without a box-like surface (adapted from Mackay and Mackay 2002).

pinched in, rather, roughly quadrate, trapezoidal or heptagonal in shape; clypeal fossae shallow, narrower (Figure 1.9) ..... **6**

**4a** Worker with few erect or suberect setae visible in profile; mesonotum and propodeum with few to no standing setae, erect setae patchy when present ..... **5**

**4b** Worker with numerous erect or suberect setae about evenly distributed over entire dorsal profile, including the mesonotum and propodeum ..... ***obscuriventris***

**5a** Dorsal profile with scattered, moderately abundant pilosity; western mountain states and Canadian provinces ..... ***laeviceps***

**5b** Dorsal profile lacking or with very few erect setae (Figure 1.10); prairie states north to Alberta and east to New England and Canadian Maritime provinces ..... ***fossaceps***

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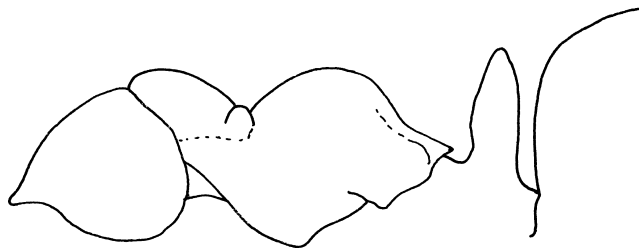


*Figure 1.10* Side view of a paratype worker of *F. fossaceps* (adapted from Mackay and Mackay 2002).

**6a** Dorsal profile with numerous erect or suberect setae about evenly distributed on head vertex, pronotum, mesonotum and propodeum ..... **7**

**6b** Dorsal profile with few erect or suberect setae on vertex, and especially, with patchy, few and scattered, or no erect setae on mesonotum and propodeum ..... **8**

**7a** Legs red, matching or at most only slightly browner than mesosoma; all sizes of workers bicoloured, without infuscation; dorsal surfaces of middle and hind tibiae with abundant, long, suberect pilosity ..... ***coloradensis***

**7b** Legs blackish; workers infuscated to varying degrees ranging from symmetrical dark dorsal blotches to blackening of all tagmata; dorsal surfaces of middle and hind tibiae with variable but short, suberect pilosity, or this sometimes almost lacking ... ***obscuripes*** (as conceived here, *obscuripes* includes questionably distinct taxon *planipilis*)

**8a** Erect setae absent or at most very few and irregularly scattered on upper surface of head, mesosoma and petiole ..... **9**

**8b** Erect setae present and approximately evenly spaced on at least dorsum of pronotum and propodeum ..... **11**

**9a** Completely or largely non-shiny species; sides and venter of head and dorsum of gaster opaque to subopaque; gaster densely pubescent and greyish ..... **10**

**9b** Shinier species: at least sides and venter of head and dorsum of gaster shiny; gaster pubescence sparser, not completely obscuring view of integument ..... ***subnitens***

**10a** Compound eyes with a few, short, fine erect setae arising among the facets; western North America (as far east as the Dakotas and New Mexico) (Figure 1.11) ..... ***ravida***

**10b** Compound eyes without erect setae; eastern United States (as far west as Wisconsin and Mississippi) ..... ***integra***

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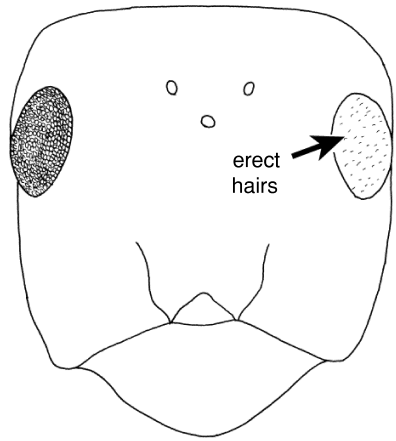



*Figure 1.11* Head of a cotype worker of *F. ravida* showing the erect hairs on the eyes (adapted from Mackay and Mackay 2002).

**11a** Gaster clothed with close-set, short erect setae that give the appearance in profile of a loose, plush-like investiture ..... **12**

**11b** Gaster with erect setae more widely spaced and not forming an even investiture ..... **14**

**12a** Underside of head with numerous erect setae, usually >10 (Figure 1.12) ..... **13**

**12b** Underside of head usually devoid of erect setae, usually <4 (Figure 1.13) ..... ***ciliata***

**13a** Standing setae of gaster longer, >0.10 mm; smaller species, major workers usually <7.0 mm total length (Figure 1.14) ..... ***mucescens***

**13b** Standing setae of gaster shorter, <0.06 mm; larger species, major workers >8.0 mm total length (Figure 1.15) ..... ***comata***

**14a** Gastral tergites lacking or with very few erect setae (sometimes a few near the anterior face of first tergite) ..... **15**

**14b** Gastral tergites with erect setae more abundant and usually more evenly distributed ..... **17**

**15a** Pronotum and angle of propodeum with numerous erect setae; gastral dorsum lacking erect pilosity, even at the rear margins of tergites, but venter with abundant, flexuous pilosity; Midwestern US grassland and open oak woodland species ..... **16**

**15b** Pronotum and propodeum lacking pilosity; gastral dorsum with a few erect setae, especially at the rear margins of tergites, and a similar array ventrally; grassland from western Dakotas to base of Rocky Mountains ..... ***criniventris***

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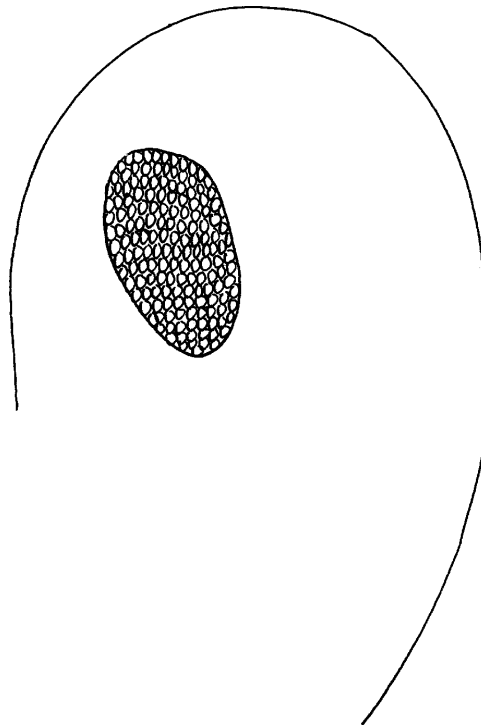


*Figure 1.12* Side view of the head of a worker of *F. ciliata* showing the lack of erect hairs on the ventral surface of the head (adapted from Mackay and Mackay 2002).

**16a** Anterior clypeal margin and mandibles with numerous coarse, flexuous, setae, Ohio west to Wisconsin and south western Iowa ..... ***prociliata***
**16b** Anterior clypeal margin and mandibles with only a few, short inconspicuous, setae, known only from northern Illinois ..... ***ferocula***
**17a** Standing setae of gastral tergites tapering, pointed at tip ..... **18**
**17b** Standing setae of gastral tergites flattened, blunt at tip ..... ***calviceps***
**18a** Vertex margin and sides of head lacking erect setae ..... ***propinqua***
**18b** Vertex margin and sides of head with numerous erect setae at least to the level of the eyes ..... ***integroides***

## Habitat and distribution

Most Palearctic wood ants are associated with heterogeneous coniferous or deciduous forests where canopy gaps allow sunlight to penetrate

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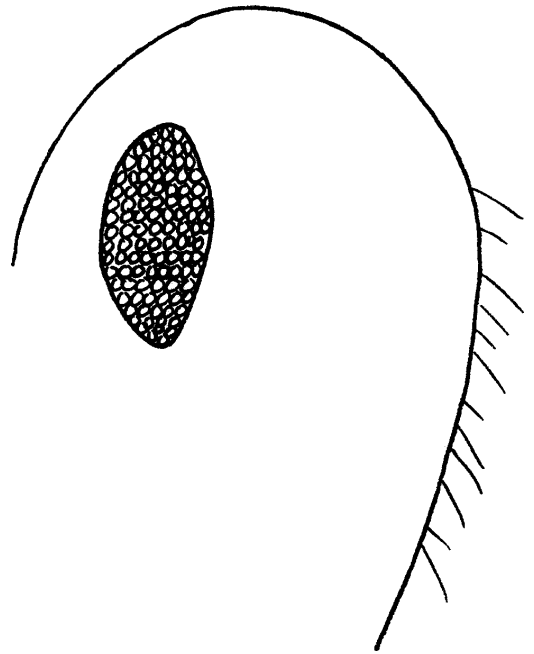


*Figure 1.13* Side view of the head of a worker of *F. comata* showing the numerous hairs on the ventral surface of the head (adapted from Mackay and Mackay 2002).

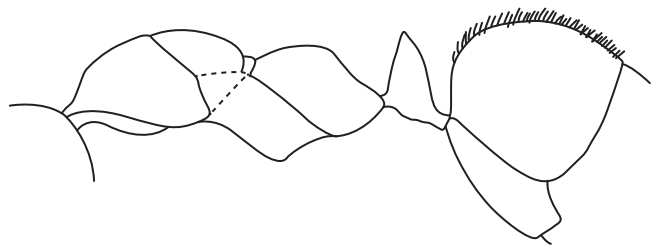


*Figure 1.14* Side view of a cotype worker of *F. mucescens* showing the longer, erect hairs on the dorsum of the gaster (adapted from Mackay and Mackay 2002).

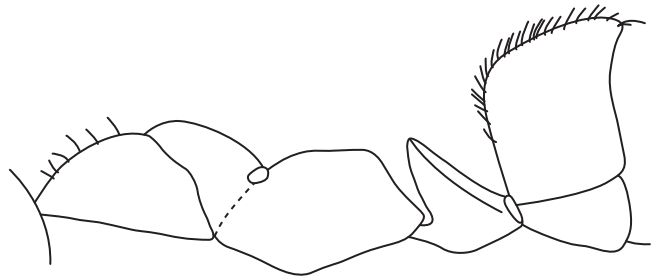


*Figure 1.15* Side view of a cotype worker of *F. comata* showing the shorter, erect hairs on the dorsum of the gaster (adapted from Mackay and Mackay 2002).

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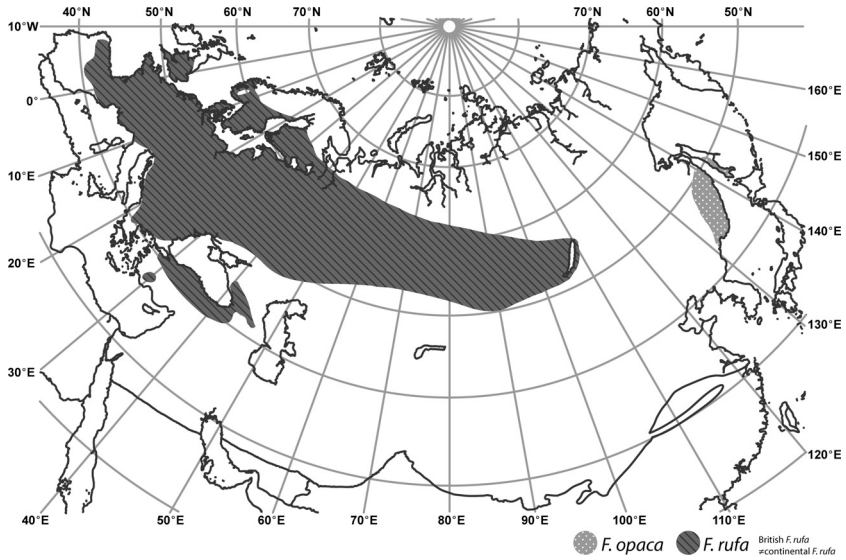



*Figure 1.16* Distributions of *Formica rufa* and *Formica opaca*. The empty area in South Norway is a genuine absence: it indicates the high Fjäll where *rufa* is absent for climatic reasons. Dlussky (1967) showed a distribution to the Russian Far East but there is no verified record east of Lake Baikal. The deviating populations in Britain and Asia Minor, which are phenotypically intermediate between the typical *polyctena* and *rufa* condition (hybridogenous?) are provisionally considered as conspecific, in the absence of convincing evidence to the contrary.

*Note for Figures 1.16–1.26*: These distribution maps integrate the sum of historical and present findings and include areas with populations that have gone extinct within the last 50 years. Range margin drawing error is <50 km.

to the forest floor. *Formica truncorum* and *F. frontalis* are usually found on forest edges and into heathland. The most xerothermic member of the group, *F. pratensis,* inhabits both woodland and woodland–steppe habitats. Though species such as *F. prociliata* and *F. ferocula* can be found in deciduous woodlands, Nearctic species are more generally associated with grassland and shrub steppe habitats. Precise habitat preferences of species can differ across their range. For example, *F. aquilonia* in Central Europe is only found between 550 and 2100 m elevation, while at higher latitudes such as in Finland and Scotland, it is rarely found above 550 m. Despite being relatively well studied in some parts of Europe, the distributions of red wood ants are not well known at a global scale. The distributions shown here for Nearctic species (Figures 1.16 to 1.26) and Palearctic species (Figures 1.27 to 1.45) are based on regional faunas and expert opinion.

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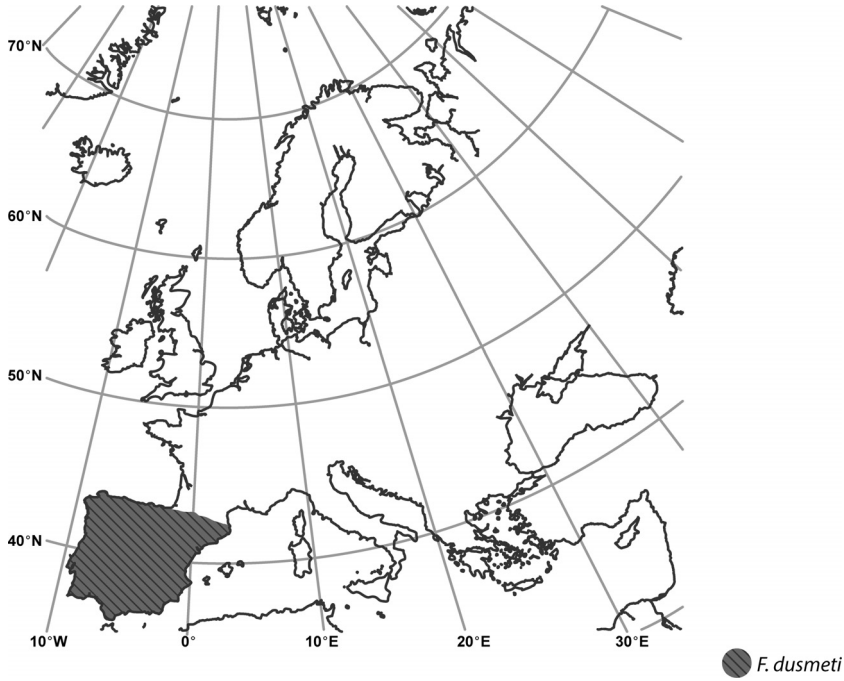



*Figure 1.17* Distribution of *Formica dusmeti*.

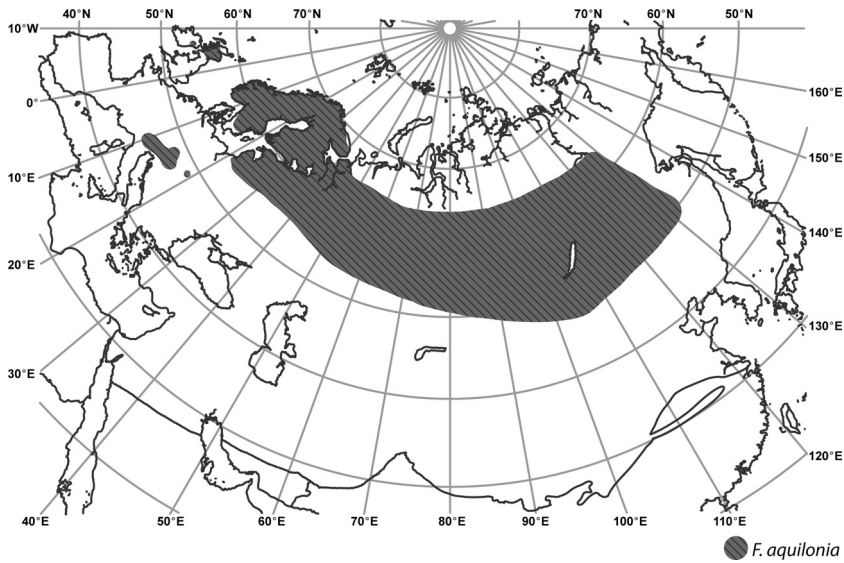



*Figure 1.18* Distribution of *Formica aquilonia*.

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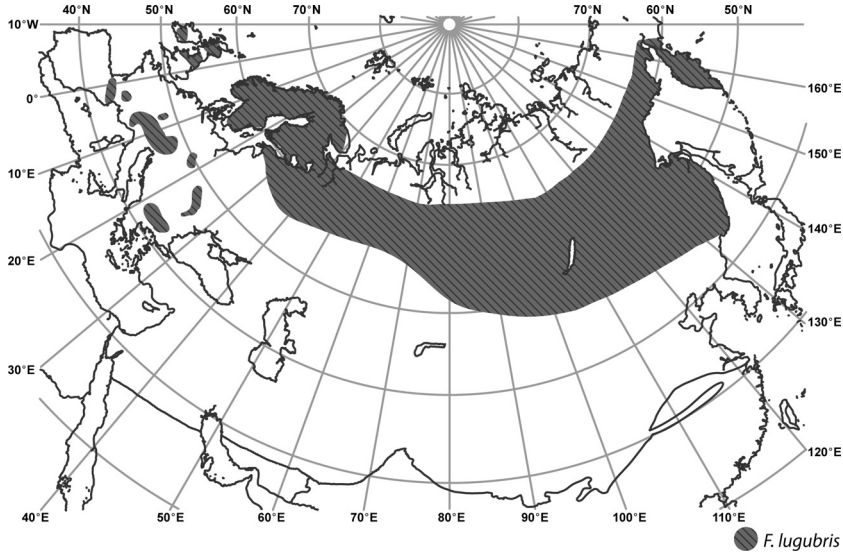



*Figure 1.19* Distribution of *Formica lugubris*.

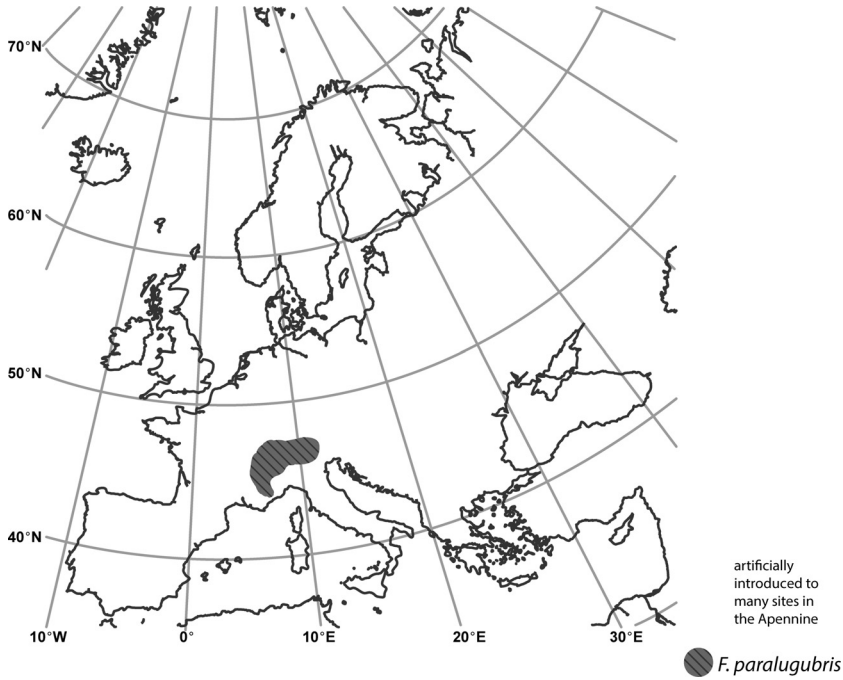



*Figure 1.20* Distribution of *Formica paralugubris*. While the native range is restricted to the western Alps, it has been artificially introduced to many places in Italy, as far south as Sicily. The survival of these introductions is unknown.

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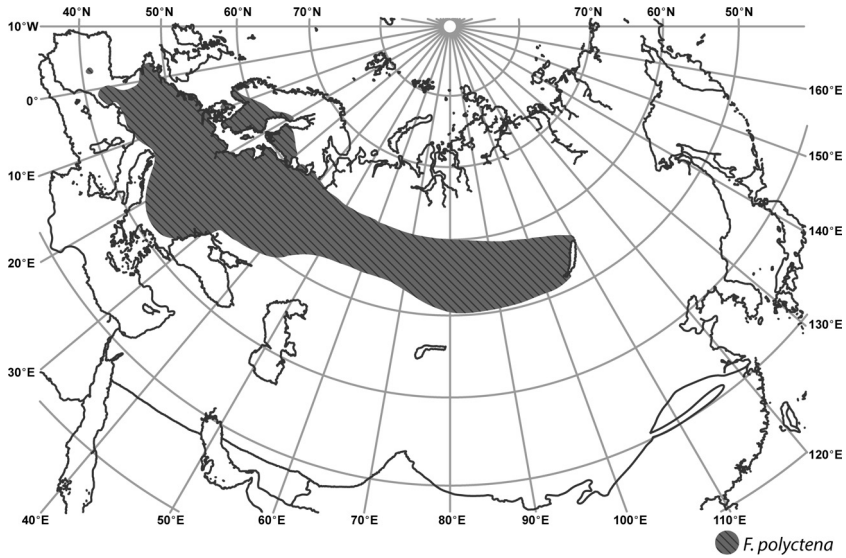



*Figure 1.21* Distribution of *Formica polyctena*. Note that Dlussky (1967) showed a distribution to the Russian Far East but there is no verified record east of Lake Baikal. This error is due to confusion with *aquilonia*.

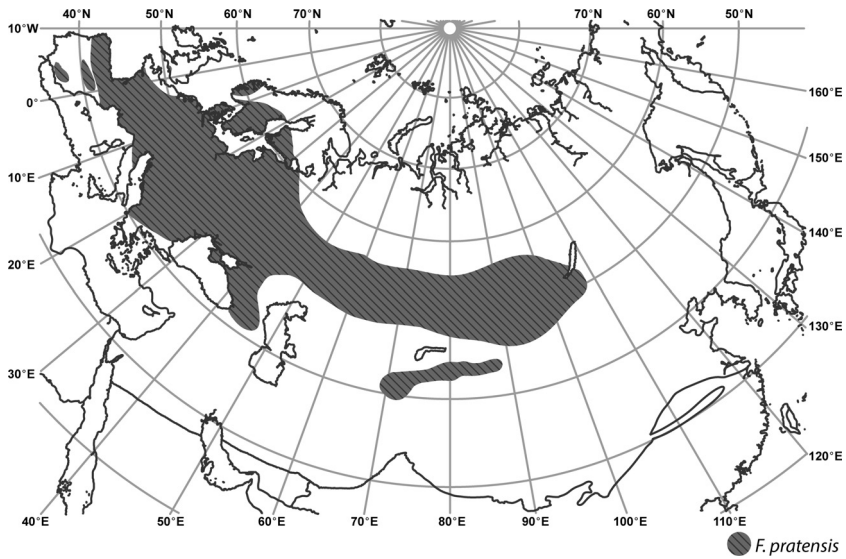



*Figure 1.22* Distribution of *Formica pratensis*.

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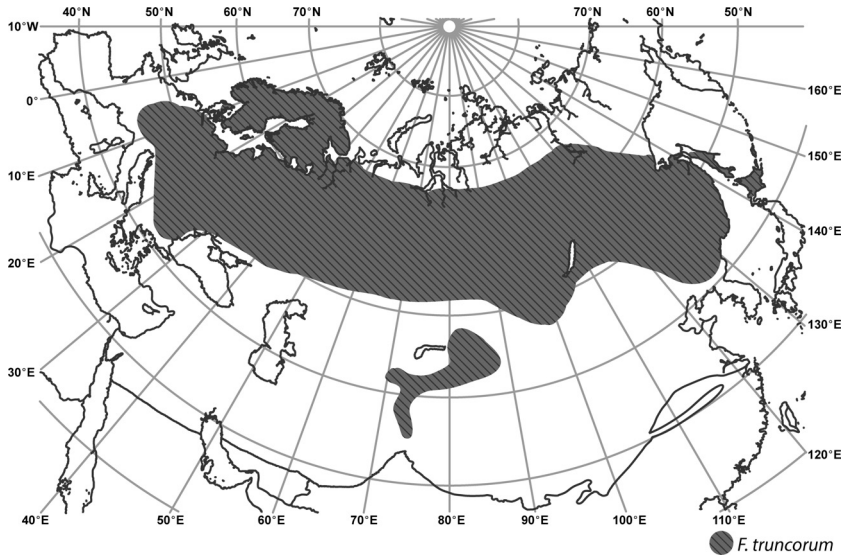



*Figure 1.23* Distribution of *Formica truncorum*.

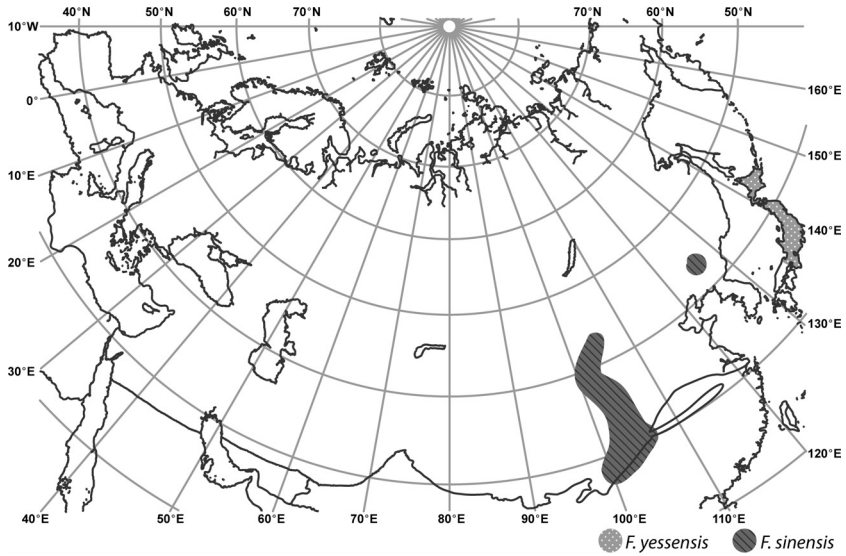



*Figure 1.24* Distributions of *Formica sinensis* and *Formica yessensis*.

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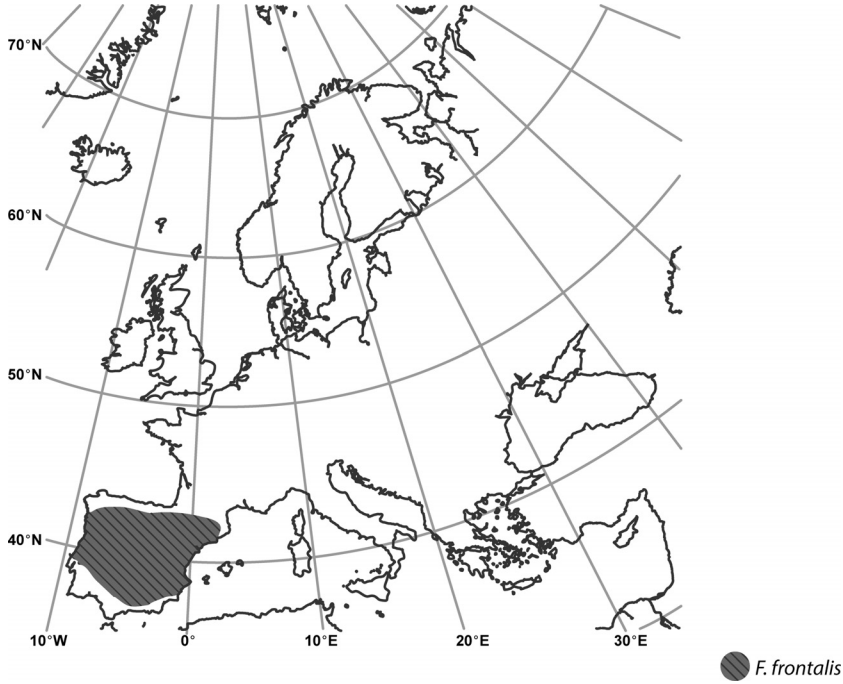



*Figure 1.25* Distribution of *Formica frontalis*.

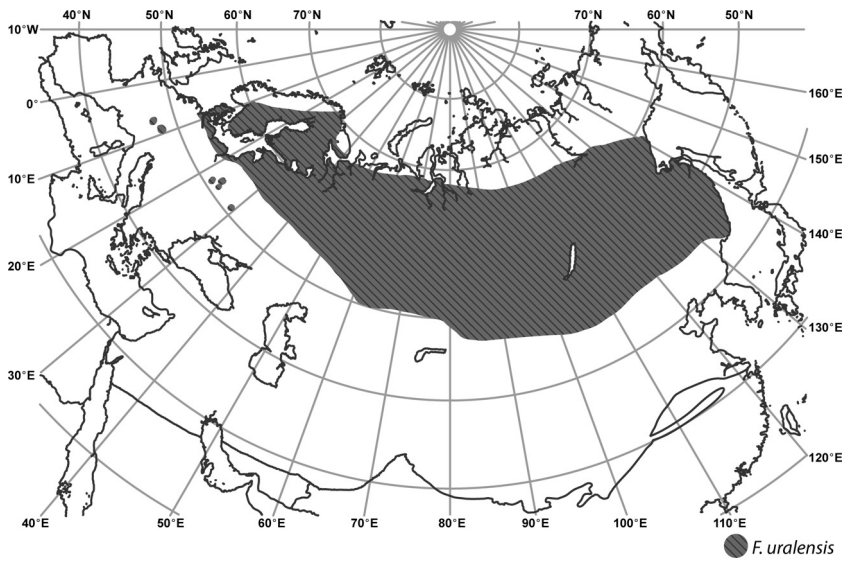



*Figure 1.26* Distribution of *Formica uralensis*.

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*Figure 1.27* North American States in which *Formica calviceps* is present.




*Figure 1.28* North American States in which *Formica ciliata* is present.

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*Figure 1.29* North American States in which *Formica coloradensis* is present.

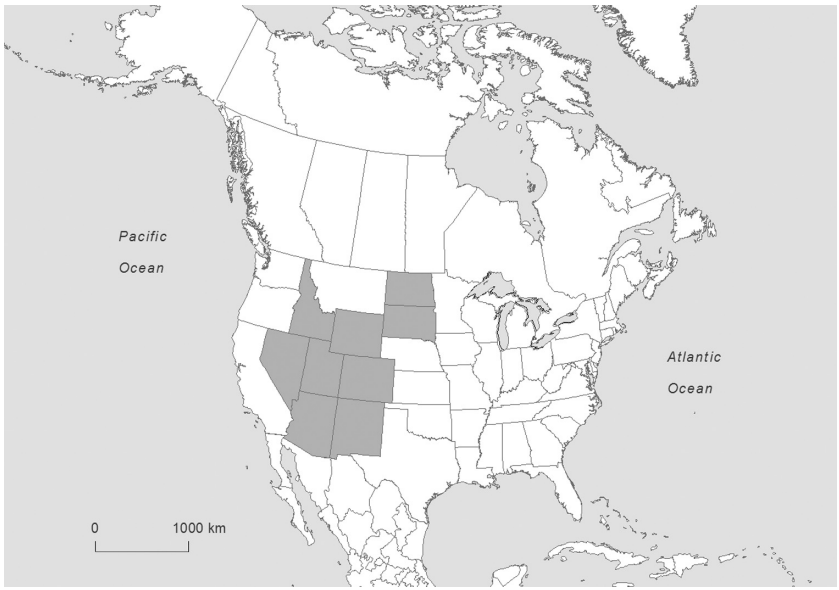



*Figure 1.30* North American States in which *Formica comata* is present.

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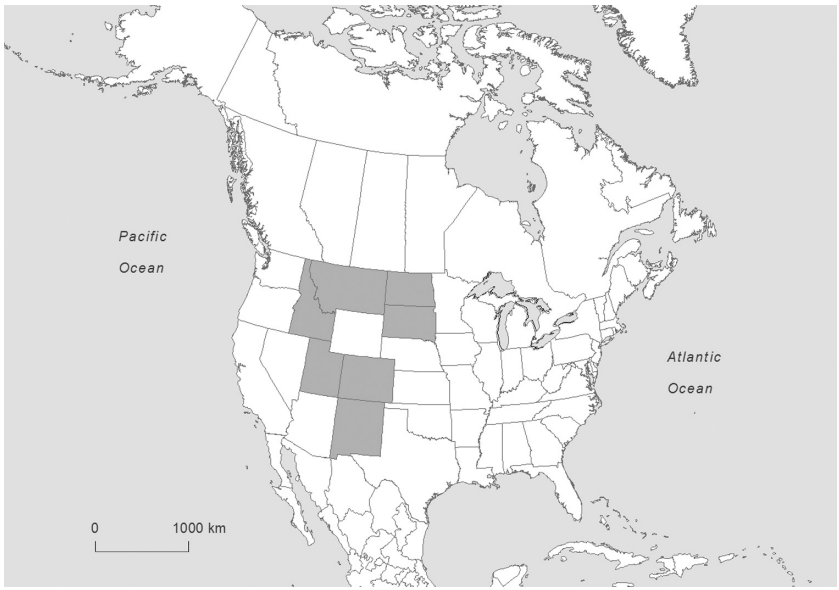



*Figure 1.31* North American States in which *Formica criniventris* is present.




*Figure 1.32* North American States in which *Formica ferocula* is present.

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*Figure 1.33* North American States in which *Formica fossaceps* is present.




*Figure 1.34* North American States in which *Formica integra* is present.

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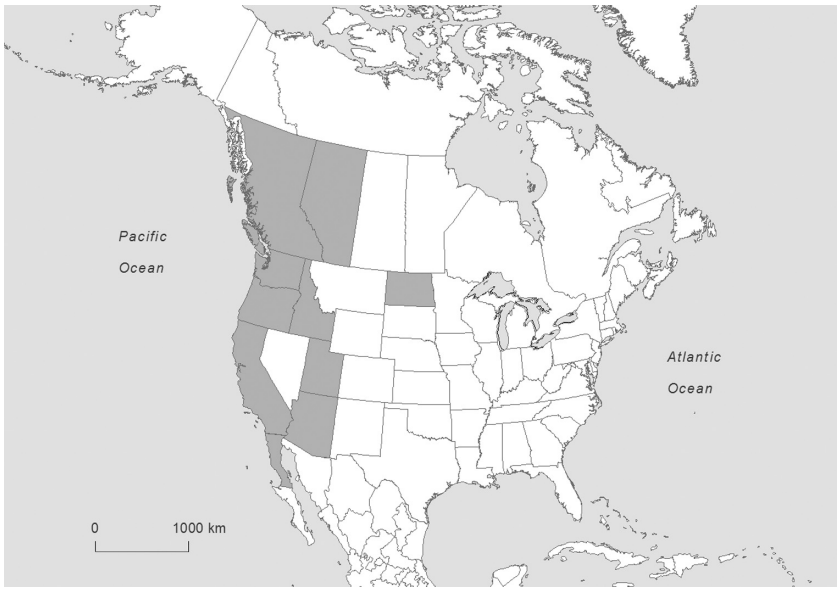



*Figure 1.35* North American States in which *Formica integroides* is present.

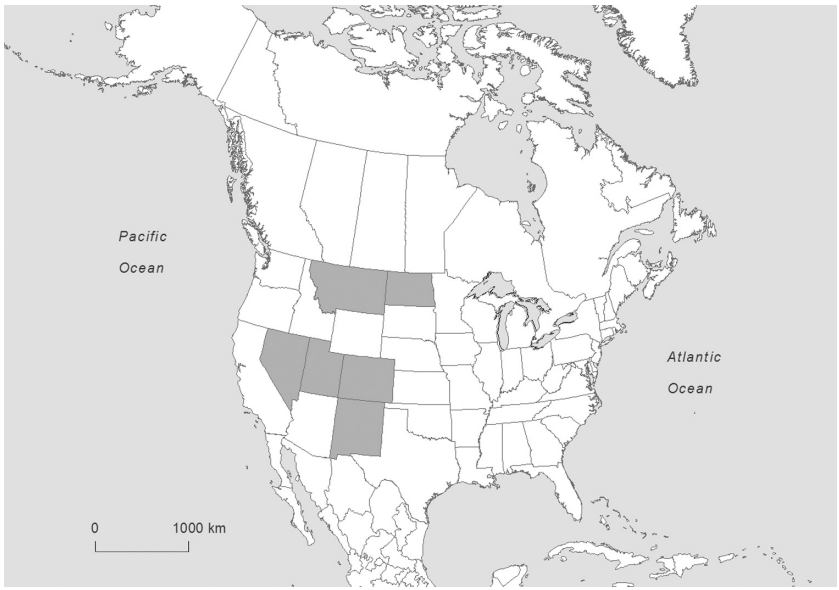



*Figure 1.36* North American States in which *Formica laeviceps* is present.

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*Figure 1.37* North American States in which *Formica mucescens* is present.

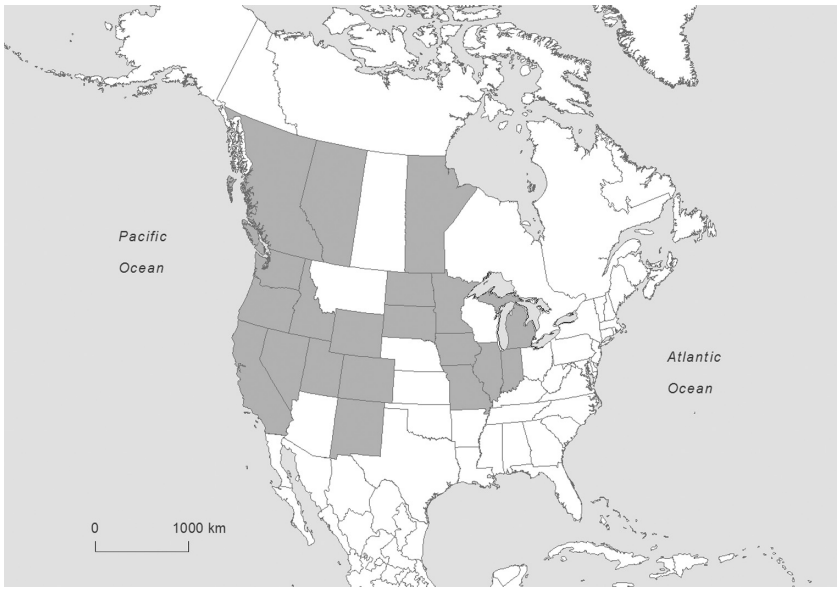



*Figure 1.38* North American States in which *Formica obscuripes* is present.

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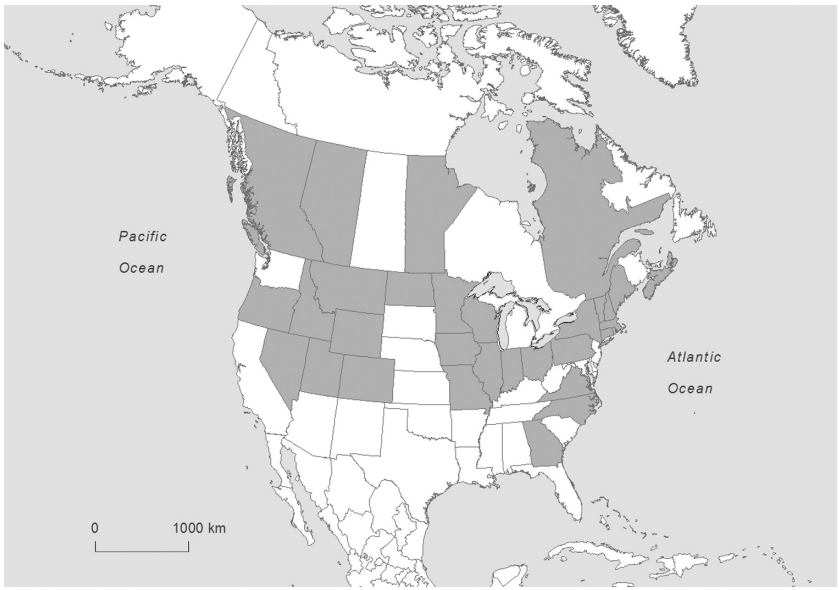



*Figure 1.39* North American States in which *Formica obscuriventris* is present.




*Figure 1.40* North American States in which *Formica oreas* is present.

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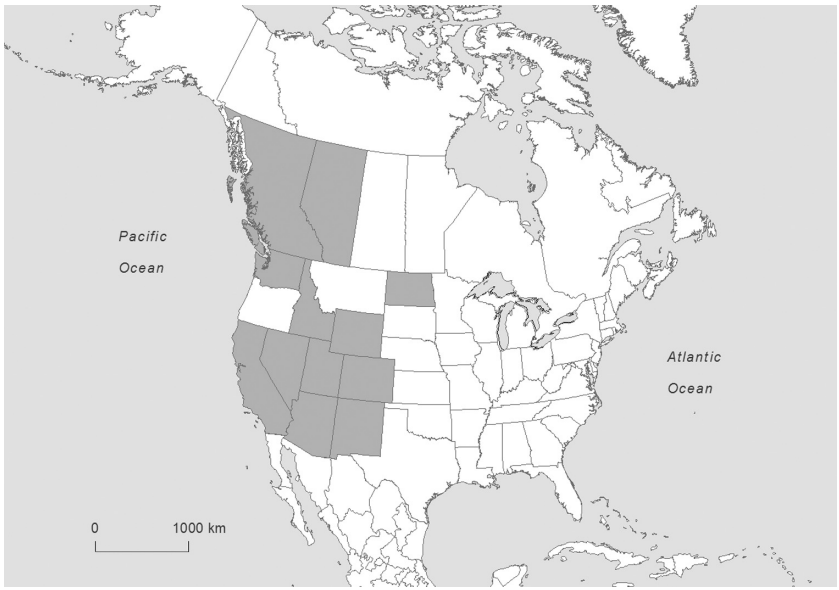



*Figure 1.41* North American States in which *Formica planipilis* is present.




*Figure 1.42* North American States in which *Formica prociliata* is present.

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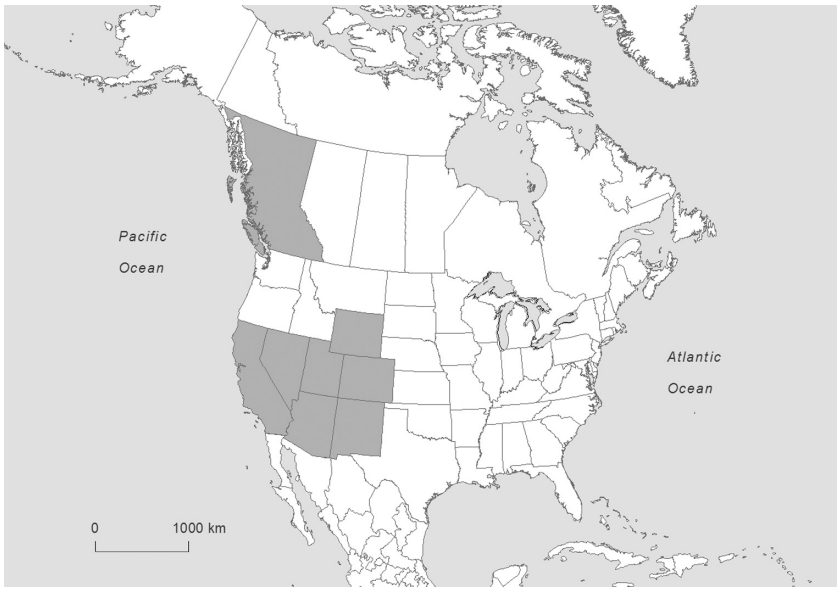



*Figure 1.43* North American States in which *Formica propinqua* is present.

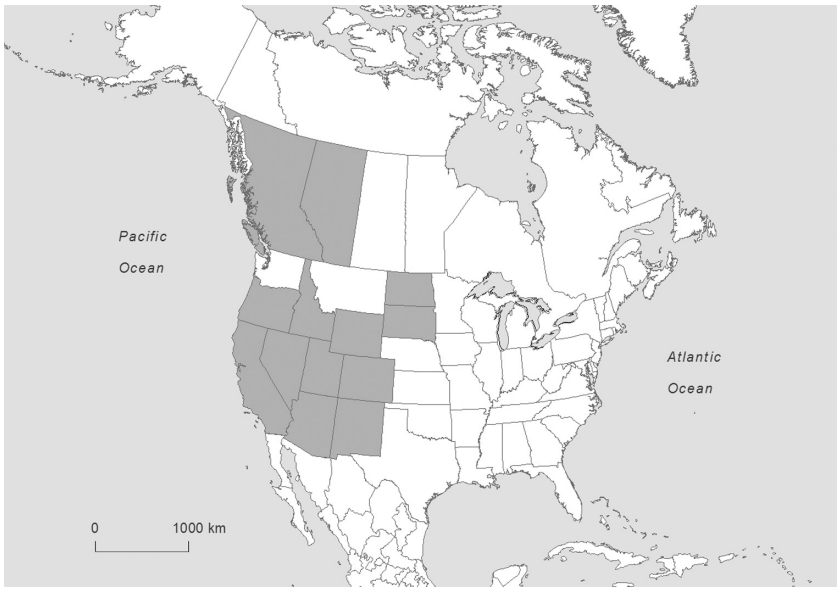



*Figure 1.44* North American States in which *Formica ravida* is present.

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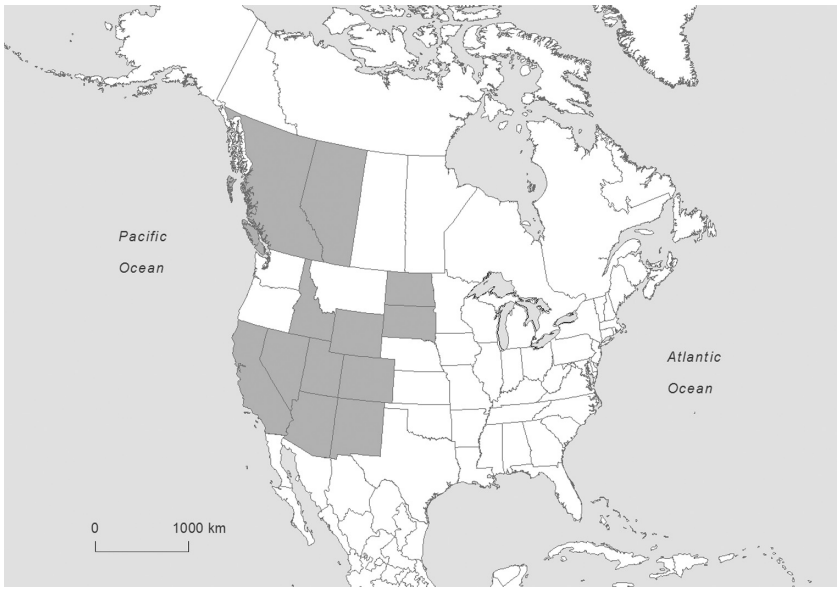



*Figure 1.45* North American States in which *Formica subnitens* is present.

## Red wood ants as social insects

Wood ants, like all ant species, are eusocial: they show communal living, cooperative brood care, overlap of generations and reproductive division of labour. In *Formica* species, workers cannot mate but are able to lay haploid male eggs, while mated females, queens, can produce both haploid male and diploid female eggs (Chapter 2). Many generations of queens and workers can coexist in the same wood ant nest, and cooperative brood care is performed by workers who groom, feed and transport the brood produced by the queens. Wood ants are ideal model systems for studying the evolution of sociality by testing the kin selection predictions of inclusive fitness theory, because red wood ants show variation in key social traits such as number of queens per nest and number of times each queen mates. These traits have knock-on effects for the evolution of social behaviours including control of worker reproduction (Chapter 2), queen–worker conflict over offspring sex ratio (Chapter 3) and kin recognition (Chapter 5). In addition to reproductive division of labour, task specialisation among workers is also seen in many social insects. Wood ants illustrate this worker division of labour with, for example, persistent foragers showing high levels of spatial specialisation (Chapter 7). Division

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of labour is thought to be one of the reasons for the success of the social insects and their ability to dominate a range of environments (Oster and Wilson 1978). Wood ants are impressive examples of ecologically successful and dominant species, having profound effects on the ecosystems in which they occur (Chapters 6, 7, 8 and 9).

## Conclusion

The large size of wood ant colonies makes their nests and busy foraging trails an obvious feature of woodlands they inhabit, leading to a long history of study of this group (e.g. Forel 1874; Donisthorpe 1915; Lubbock 1929; Weber 1935). Currently, around 15 research groups worldwide are concerned, to a greater or lesser extent, with the study of wood ants in the context of ecology and conservation. However, the distribution of researchers is strongly predisposed to Europe and, in particular, Western Europe, with studies in Finland and Switzerland predominating. There is therefore bias in focal species, the nature and management of habitats and the issues studied. To understand fully the importance and relevance of wood ants on a global scale, investigation of wood ants beyond Europe is needed. Furthermore, the dominance and distinctiveness of wood ants make them an ideal 'charismatic species group' for engaging the public in issues of woodland management and conservation.

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