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Edited by Jenni A. Stockan and Elva J. H. Robinson

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

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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 km². 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

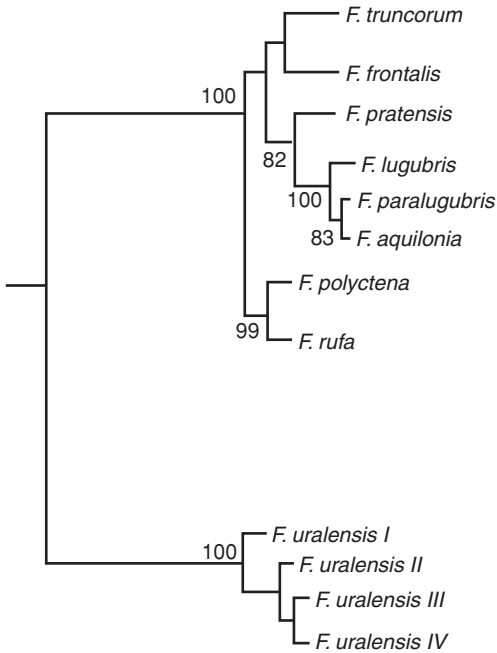


Figure 1.1 Phylogenetic cladogram of Eurasian wood ant species based on mitochondrial cytochrome *b* sequences (redrawn with permission from Goropashnaya *et al.* 2012).

1991; Czechowski 1996). The *F. rufa/polycytena* 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*, *polycтена* 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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[More information](#)Table 1.1 *Species currently considered members of the subgenus Formica s. str. group.*

Palaearctic species	Nearctic species
^a <i>Formica rufa</i> Linnaeus 1761	<i>Formica calviceps</i> Cole 1954
<i>Formica dusmeti</i> Emery 1909	<i>Formica ciliata</i> Mayr 1886
^a <i>Formica aquilonia</i> Yarrow 1955	<i>Formica coloradensis</i> Creighton 1940
^a <i>Formica lugubris</i> Zetterstedt 1838	<i>Formica comata</i> Wheeler 1909
<i>Formica paralugubris</i> Seifert 1996	<i>Formica criniventris</i> Wheeler 1912
^a <i>Formica polycтена</i> Förster 1850	<i>Formica ferocula</i> Wheeler 1913
^a <i>Formica pratensis</i> Retzius 1783	<i>Formica fossiceps</i> Buren 1942
<i>Formica truncorum</i> Fabricius 1804	<i>Formica integra</i> Nylander 1856
<i>Formica sinensis</i> Wheeler 1913	<i>Formica integroides</i> Emery 1913
<i>Formica frontalis</i> Santschi 1909	<i>Formica laeviceps</i> Creighton 1940
<i>Formica yessensis</i> Forel 1901	<i>Formica mucescens</i> Wheeler 1913
^a <i>Formica uralensis</i> Ruzsky 1895	<i>Formica obscuripes</i> Forel 1886
<i>Formica opaca</i> Nylander 1856	<i>Formica obscuriventris</i> Mayr 1970
	<i>Formica oreas</i> Wheeler 1903
	^b <i>Formica planipilis</i> Creighton 1940
	^c <i>Formica proclivata</i> Kennedy and Dennis 1937
	<i>Formica propinqua</i> Creighton 1940
	<i>Formica ravida</i> Creighton 1940
	<i>Formica subnitens</i> 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 Palaearctic 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 $\geq \times 150$. 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. Proprioceptive 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.

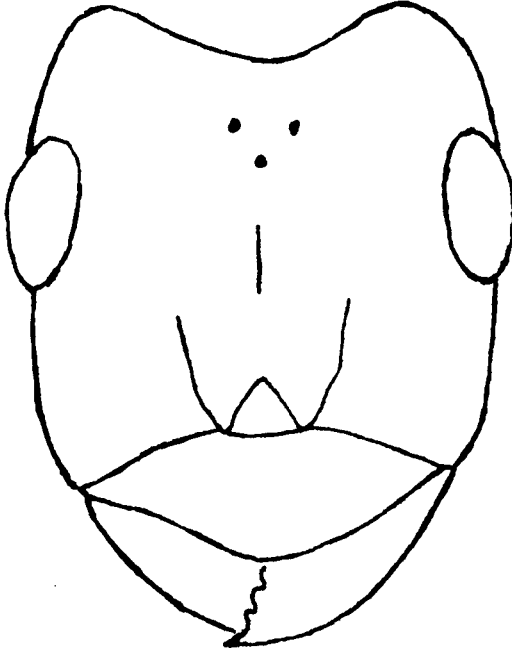


Figure: 1.3 Head of a *Coptoformica* worker showing the clearly excavated posterior margin of the head.

nSc – unilateral setae number on dorsal plane of scape.

SL – maximum scape length, excluding articular 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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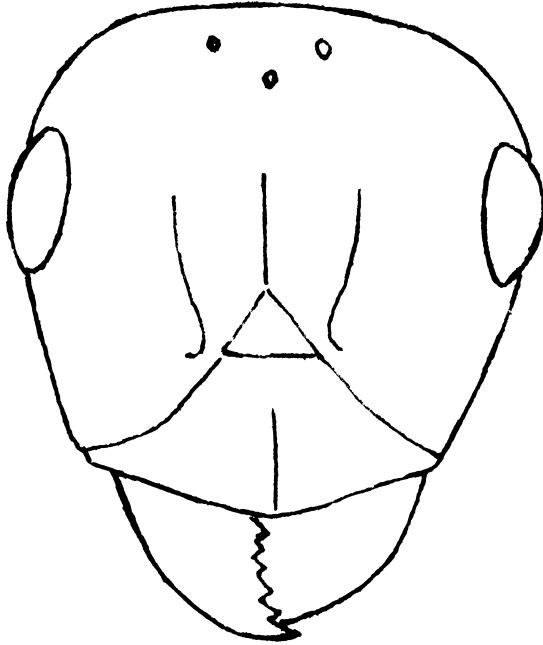


Figure 1.4 Head of a worker with a straight posterior margin of the head.

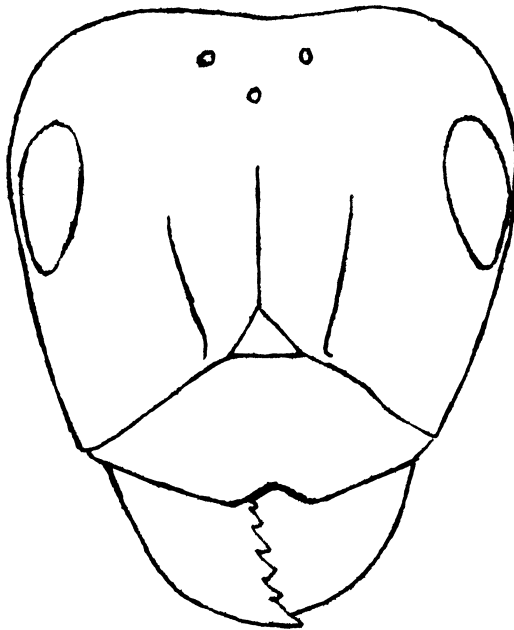


Figure 1.5 *Raptiformica* worker head showing only weakly excavated posterior margin and emarginated clypeus.

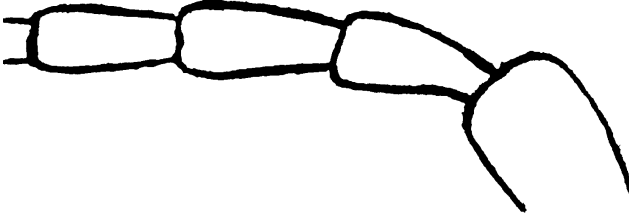


Figure 1.6 Funiculus of antenna showing 2nd and 3rd segments at least twice as long as wide.



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*