

Worldwide spread of the ruby ant, *Myrmica rubra* (Hymenoptera: Formicidae)

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Abstract

The ruby ant, *Myrmica rubra* (LINNAEUS, 1758) (formerly *Myrmica laevinodis* NYLANDER, 1846), an aggressive Eurasian species with a powerful sting, is now spreading through temperate North America. To document the worldwide distribution of *M. rubra* and evaluate its potential for further spread, we compiled published and unpublished specimen records from > 2000 sites. We report the earliest known *M. rubra* records for 71 geographic areas (countries, major islands, US states, Canadian provinces, and Russian federal districts), including three areas with no previously published records: Prince Edward Island, Washington State, and the Far Eastern Federal District of Russia. All earlier published records of *M. rubra* from East Asia, including the Far East of Russia, Japan, and China, appear to be misidentifications of *Myrmica kotokui* FOREL, 1911.

Myrmica rubra is native to an enormous expanse extending from Ireland and Portugal in westernmost Europe across 8000 km to central Asia and eastern Siberia, and from 39 to 70° N in latitude. Exotic populations of *M. rubra* were first recorded in eastern North America more than 100 years ago. *Myrmica rubra* is now documented from five southeastern Canadian provinces (New Brunswick, Nova Scotia, Ontario, Prince Edward Island, and Quebec), six northeastern US states (Maine, Massachusetts, New Hampshire, New York, Rhode Island, and Vermont), and one northwestern state (Washington) ranging from 41.5 to 47.6° N.

Given the vast range of *M. rubra* in Eurasia, perhaps the most striking aspect about this species in North America is how little it has spread over the past century. Most North American records of *M. rubra*, however, date from the last ten years, suggesting these North American populations are expanding. There appear to be no geographic barriers that would prevent *M. rubra* from spreading across the US and Canada, from coast to coast.

Key words: Biogeography, biological invasion, exotic species, invasive species, stinging ant.

Myrmecol. News 14: 87-96 (online 26 August 2010)
ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 26 January 2010; revision received 29 April 2010; accepted 29 April 2010

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Introduction

Numerous ant species have spread around the world through human commerce. Only a few of these are known to have significant ecological and / or economic impacts. Most of the destructive invasive ants have spread through tropical and subtropical regions, often achieving extremely broad distributions in both the Old and New World, e.g., *Monomorium destructor* (JERDON, 1851), *Pheidole megacephala* (FABRICIUS, 1793) and *Linepithema humile* (MAYR, 1868) (WETTERER 2007, 2009, WETTERER & al. 2009). One potentially destructive Eurasian ant now spreading through temperate North America is the ruby ant, *Myrmica rubra* (LINNAEUS, 1758). Reporting this ant from Massachusetts, WHEELER (1908) wrote that *M. rubra* (as its junior synonym *Myrmica laevinodis* NYLANDER, 1846) "is the most disagreeable of the palaearctic Myrmicas ... its workers are aggressive and sting severely. It is very fond of attending aphids and, unlike our timid native Myrmicas, which live in the retirement of woods, bogs, heaths and waste places generally, it prefers to nest in cultivated soil. Hence it may be-

come a nuisance in lawns and dooryards." Here, we document the worldwide distribution of *M. rubra* and speculate on its future spread.

Taxonomy and identification: *Myrmica rubra* has reddish-brown monomorphic workers (4 - 5 mm total length; Figs. 1 - 3). Most strikingly, "*M. rubra* is a very aggressive species which stings freely" (SEIFERT 1988). COLLINGWOOD (1987) wrote that *M. rubra* "has the most vicious sting of all the British ants, comparable with that from a stinging nettle."

LINNAEUS (1758) first described *Formica rubra* (= *M. rubra*) from Europe. LINNAEUS (1767) later added "pessime nostratum pungit" (= "it stings the worst of our native species") to its description. Unfortunately, LINNAEUS' (1758, 1767) written description matched more than one ant species. It was generally presumed that *M. rubra* was the senior synonym of either *Myrmica ruginodis* NYLANDER, 1846 or *Myrmica laevinodis* NYLANDER, 1846 (sometimes spelled *levinodis*), because these two European species have the

most powerful stings (EMERY 1908, DONISTHORPE 1913, 1915). Some authors considered these to be two subspecies of *M. rubra*, with no nominal subspecies (i.e., *M. rubra rubra*). SANTSCI (1931) speculated (incorrectly) that *M. rubra* was the senior synonym of *M. ruginodis*, and many researchers accepted this judgment (e.g., WEBER 1947, BRIAN & BRIAN 1949, CREIGHTON 1950). This error was corrected when YARROW (1955) examined all *Myrmica* specimens in the Linnaean type collection and concluded that the type of *M. rubra* was actually the senior synonym of *M. laevinodis*. Thus, all published records of *M. laevinodis* refer to *M. rubra*. A few pre-1955 records of *M. rubra*, however, actually refer to *M. ruginodis*, but these can be readily recognized if an author refers to *M. laevinodis* and *M. rubra* as distinct species (e.g., BRIAN & BRIAN 1949).

Junior synonyms of *M. rubra* include *M. laevinodis* (described from Finland and Sweden; synonymized with *M. rubra* by YARROW 1955), *Myrmica longiscapus* CURTIS, 1854 (described from Scotland and England; synonymized with *M. laevinodis* by MAYR 1863), *Myrmica laevinodis europaea* FINZI, 1926 (first available use of *Myrmica rubra* ssp. *champlaini* var. *europaea* FOREL, 1911) (described from Norway; synonymized with *M. rubra* by RADCHENKO & al. 1997), *Myrmica laevinodis bruesi* WEBER, 1947 (first available use of *Myrmica rubra laevinodis* var. *bruesi* WHEELER, 1906) (described from Massachusetts; synonymized with *M. laevinodis* by CREIGHTON 1950), and *Myrmica microrubra* SEIFERT, 1993 (described from Germany; synonymized with *M. rubra* by STEINER & al. 2006). One extant subspecies, *Myrmica rubra neolaevinodis* FOREL, 1901, was described from specimens intercepted in New York on flowers imported from Hamburg, Germany.

PROVANCHER (1887) synonymized *Myrmica incompleta* PROVANCHER, 1881 (described from Canada) with *M. laevinodis* (= *M. rubra*). FRANCOEUR & BEIQUE (1966), however, revived *M. incompleta*, recognizing it as the senior synonym of *Myrmica brevinodis* EMERY, 1895, a species known from across Canada and the northern US. SMITH (1951) synonymized *Myrmica rubra champlaini* FOREL, 1901 (described from Quebec) with *M. laevinodis*, but GRODEN & al. (2005) instead synonymized it with *Myrmica brevispinosa* WHEELER, 1917.

RADCHENKO (1994) placed *M. rubra* with ten other species in the *M. rubra* species-group. Within this group, *M. rubra* and *M. ruginodis* formed a clade whose sister group included the other nine species, all from Asia: *Myrmica dshungarica* RUZSKY, 1905 (described from Kazakhstan), *Myrmica tibetana* MAYR, 1889 (from Tibet), *Myrmica chinensis* VIEHMEYER, 1922 (from China), *Myrmica smythiesii* FOREL, 1901 (from India), *Myrmica juglandeti* ARNOL'DI, 1976 (from Kyrgyzstan), *Myrmica kryzhanovskii* ARNOL'DI, 1976 (from Tajikistan), *Myrmica ferganensis* FINZI, 1926 (from Kyrgyzstan), *Myrmica dicaportacoi* MENOZZI, 1939 (from India), and *Myrmica everesti* DONISTHORPE, 1929 (from near Mount Everest). After further analyses, however, A.G.R. now considers the three closest relatives of *M. rubra* to be *M. ruginodis*, *Myrmica arisana* WHEELER, 1930, and *Myrmica kotokui* FOREL, 1911 (A.G. Radchenko, unpubl.), and excludes the other species mentioned above from the *M. rubra* species-group. *Myrmica arisana* is known from Taiwan (WHEELER 1930) and *Myrmica kotokui* is

known from Japan, Korea, and the Russian Far East (COLLINGWOOD 1976, RADCHENKO 2005).

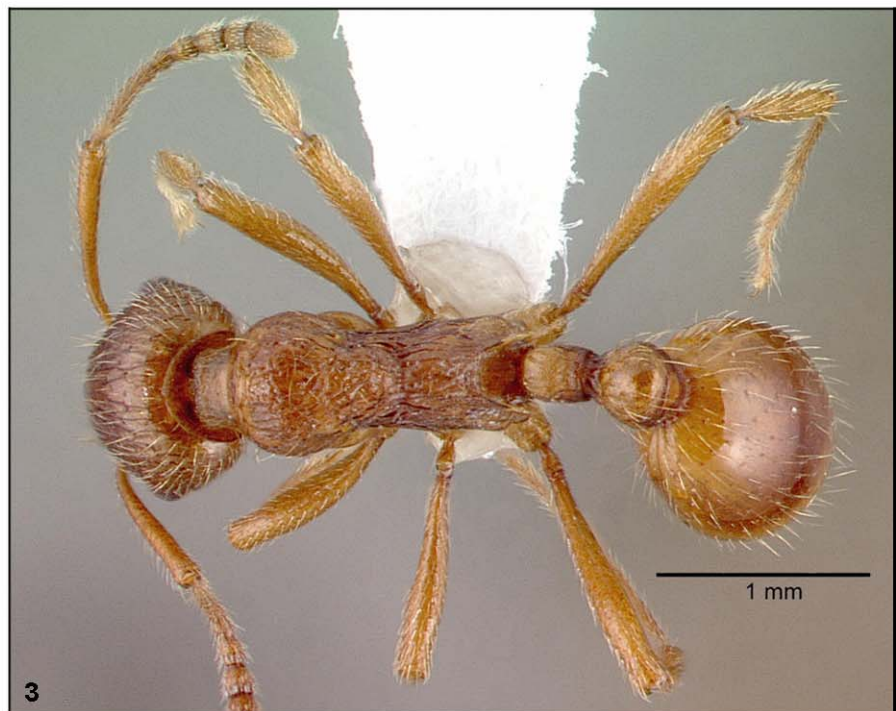
Myrmica rubra can be distinguished from *M. ruginodis* by the shape and sculpture of the petiolar node and the propodeal spine length. The petiolar node is rounded in *M. rubra*, but flat-topped in *M. ruginodis*; the sides of node are striated or at most finely rugulose in *M. rubra*, but coarsely rugose in *M. ruginodis* (*laevinodis* means "smooth node," whereas *ruginodis* means "wrinkled node.") Also, *M. rubra* has relatively shorter propodeal spines than does *M. ruginodis*. In the past, many authors recognized intermediate forms between *M. rubra* and *M. ruginodis* based on propodeal spine length. BRIAN & BRIAN (1949), however, found that propodeal spine length is correlated with worker size, such that large *M. rubra* workers have the same spine length as small *M. ruginodis* workers. BRIAN & BRIAN (1949) found that when comparing the spine length to head width ratio, *M. rubra* and *M. ruginodis* are simple to distinguish.

Common names: In Eurasia, common names for *M. rubra* include the red ant and common red ant (and their equivalents in other languages), names that are also applied to several other species. Recently, North American researchers have begun calling *M. rubra* the European red ant or European fire ant. We consider all these names to be unsatisfactory. The only distinctive name is European fire ant, and this name is misleading because it falsely suggests a kinship with "true" *Solenopsis* fire ants. In addition, *M. rubra* is not strictly European; it is also native in much of northern Asia as well, and most of its closest relatives are strictly Asian species. In Latin, *rubra* means ruby, dark red, ruddy, reddish, blushed, flushed, or shamed. We therefore suggest "ruby ant" as a new English common name for *M. rubra*.

Methods

We documented the worldwide range of *Myrmica rubra* using both published and unpublished records. We obtained unpublished site records from museum specimens in the collections of the Museum of Comparative Zoology (MCZ), Archbold Biological Station (ABS), Zoological Museum of the Moscow State University (ZMMU), Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZISP), Schmalhausen Institute of Zoology of the Ukrainian National Academy of Sciences, Kiev (SIZK), and the Museum and Institute of Zoology of the Polish Academy of Sciences, Warsaw (MIZ). Stefan Cover identified all specimens at the MCZ and ABS; A.G.R. identified all specimens at the ZMMU, ZISP, SIZK, and MIZ. In addition, we used on-line databases with collection information on specimens by Antweb (www.antweb.org) and the Global Biodiversity Information Facility (www.gbif.org). We also received unpublished records from Herbert Zettel (Czech Republic, Serbia, Slovenia), S. Tschesnokova (Russia), R. Schultz (Kazakhstan, Kyrgyzstan, and Russia), J. Huber (Canada), A. Francoeur (Canada), G. Elmes (Kazakhstan, Kyrgyzstan, and Russia), and M. Bustos (Canada).

Geographic coordinates for collection sites came from published references, specimen labels, maps, or geography web sites (e.g., earth.google.com, www.tageo.com, and www.fallingrain.com). If a site record listed a geographic region rather than a "point locale," and we had no other



Figs. 1 - 3: *Myrmica rubra*. (1) Head of worker from Italy; (2) lateral view of the same worker; (3) dorsal view of the same worker (photos by A. Nobile; copyright AntWeb.org).

record for this region, we usually used the coordinates of the largest town within the region. If one source had many sites less than 10 - 20 km apart (e.g., KOFLER 1995, SCHLICK-STEINER & STEINER 1999), we often did not plot every site.

We did not map records of *M. rubra* intercepted in shipments by quarantine inspectors, e.g., GRODEN & al.'s (2005) records of *M. rubra* found in cargo arriving in Massachusetts (from Poland), New Jersey (from Holland and England), New York (from Germany), Pennsylvania (from Ireland & Germany), and Washington DC (from Germany).

Results

We compiled published and unpublished specimen records from > 2000 sites. We documented the earliest known *M. rubra* records for 71 geographic areas (countries, major islands, US states, Canadian provinces, Russian federal districts; Tabs. 1 - 4), including the first records of *M. rubra* from Prince Edward Island (det. S. Cover), Wash-

ington (det. S. Cover), and the Far Eastern Federal District of Russia (det. A.G.R.). For five of these geographic areas, we had no specific site record, so we mapped the record to the largest city (Bosnia mapped to Sarajevo, Kaliningrad Oblast mapped to Kaliningrad), or in the case of three southern areas, we mapped a northern mountain (Koula in Greece, Monte das Raposas in Portugal, and Mahya Dagi in Thrace).

Myrmica rubra has records from a large area of the Palaearctic stretching from Ireland and Portugal in Western Europe across 8000 km to central Asia and Siberia, and spread in latitude from 39 - 70° N (> 95% of records from 40 - 65° N; Fig. 4; Tabs. 1 - 3). At lower latitudes, *M. rubra* is usually found only at higher elevations. In continental Europe, *M. rubra* is known from all countries except Albania, Monaco, and San Marino (Tabs. 1 - 3). Most *M. rubra* records come from the western part of its native range, but this appears to be largely due to greater sampling and most accessible data in Western and Central

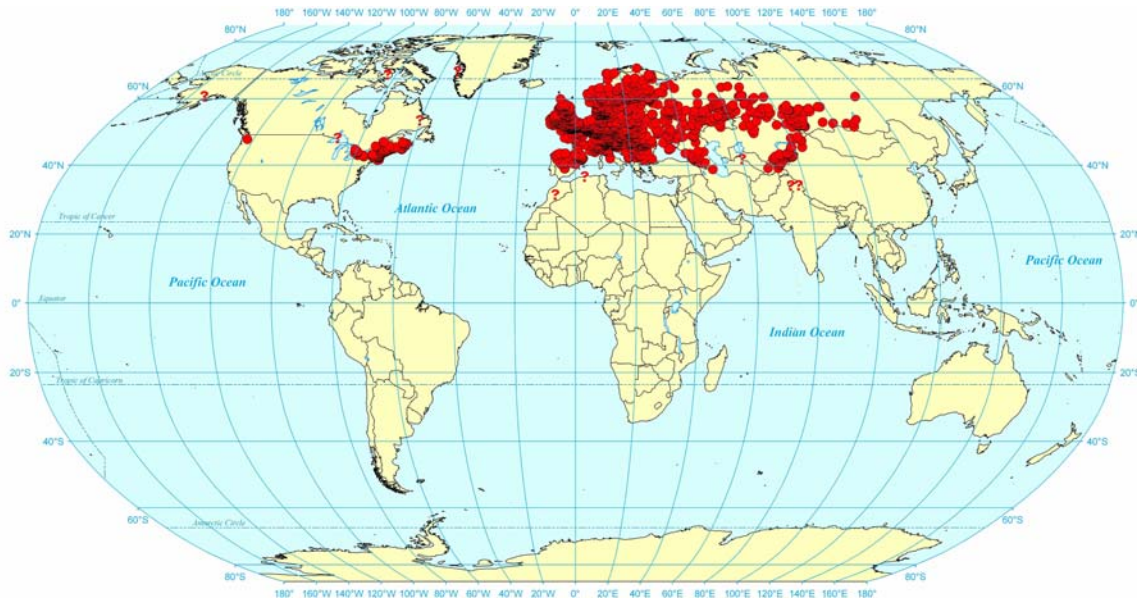


Fig. 4: Worldwide distribution records of *Myrmica rubra*. ? = questionable record (see text).

Europe. Similarly, the dates of the earliest records of *M. rubra* in different parts of its native range have little significance beyond indicating where early ant research was conducted and the results published in accessible sources.

In North America, *M. rubra* has been reliably recorded from five southeastern Canadian provinces (New Brunswick, Nova Scotia, Ontario, Prince Edward Island, and Quebec), six northeastern US states (Maine, Massachusetts, New Hampshire, New York, Rhode Island, and Vermont), and one northwestern state (Washington) (Tab. 4). Most *M. rubra* records in North America are from the past ten years.

In June 2008, J.K.W. collected *M. rubra* at eight sites on Prince Edward Island, a Canadian province where *M. rubra* has not been previously reported (geo-coordinates in parentheses): Dalvay, by hotel (46.416, -63.074), Charlottetown, Victoria Park (46.229, -63.139), Brookvale Provincial Park, forest (46.275, -63.421), Darnley, forest patch (46.546, -63.642), Brundenell River Provincial Park, by river (46.199, -62.576), Sally's Beach Provincial Park, near beach (46.264, -62.380), Seal Cove, campground (46.046, -62.523), and Portage, by bike trail (46.665, -64.058). J.K.W. also collected *M. rubra* at a highway rest area in Medway, Maine (45.596, -68.535) and on the roadside by the ferry terminal on Deer Island, New Brunswick (44.928, -66.985). The records came from a wide variety of habitats, including an urban park, the manicured grass of a hotel, beachfront scrub, and intact forest.

Questionable records: We have mapped ten questionable records from sites that fall outside the confirmed range of *M. rubra* (question marks in Fig. 4). Although we believe that all these records of *M. rubra* are probably based on errors of identification or location, we included them because they have been largely overlooked and deserved to be re-examined.

Two early voyages to Arctic Greenland and neighboring parts of North America, both listed *M. rubra* as the only ant species recorded. From an 1824 - 1825 voyage, ROSS (1826) wrote that *Formica rubra* (= *M. rubra*) was "abundant at the Whale-fish Islands; it was also found, on

the preceding voyage, on several parts of the Melville Peninsula" (in Greenland and Nunavut, respectively). From an 1829 - 1833 Arctic voyage, CURTIS (1835) listed *Myrmica rubra* as "Numerous, under stones," but gave no site information. These records, however, predate the descriptions of many related species (including *M. ruginodis*), and could be misidentifications. WEBER (1953) asserted that these records were probably misidentifications of *Formica fusca* LINNAEUS, but gave no rationale for this conclusion. However, it seems unlikely that CURTIS (1835) would confuse ants in two such fundamentally dissimilar genera, the namesakes of two subfamilies (*Myrmica* in Myrmicinae versus *Formica* in Formicinae). In fact, CURTIS (1854) described *Myrmica longiscapus* (= *M. rubra*) and wrote keys distinguishing *Myrmica* from *Formica*. It seems more likely that the ants were a species of *Myrmica* (e.g., *Myrmica alaskensis* WHEELER, 1917) or another myrmicine species (e.g., *Leptothorax acervorum* (FABRICIUS, 1793)) known from Arctic Canada and Alaska. Remarkably, we have found no other ant records of any kind from Nunavut or Greenland. In fact, recent authors commonly state that no ants now live in Greenland, though there are fossil ants from northern Greenland (e.g., BENNIKE & BÖCHER 1990, HEINZE 1993). Someone needs to go look for these ants.

ANDRÉ (1883) listed the range of *M. laevinodis* (= *M. rubra*) as including North America, though we do not know the source of this information. MAYR (1886), in his review of the ants of North America, wrote of *M. laevinodis* (= *M. rubra*): "This species is known to me only from Labrador," then reported *M. ruginodis* from Colorado and Virginia. We do not know the sources of these records. ASHMEAD (1902) reported *M. laevinodis* (= *M. rubra*) collected from Nushagak River in Alaska, noting that this species "occurs also in Siberia and various parts of the United States." Yet we have been unable to find any other record of this species from the United States published before WHEELER (1906).

We also mapped questionable records of *M. laevinodis* (= *M. rubra*) from Kashmir (FOREL 1906), North India (KARAWAJEW 1934), and Turkmenistan (KARAWAJEW 1934).

Tab. 1: Earliest known records for *Myrmica rubra* from its native range in Western Europe. ENB = inatura - Erlebnis Naturschau Dornbirn, ZMUC = University of Copenhagen Zoology Museum.

| | Earliest record |
|------------------|---|
| Andorra | 2006 (BERNADOU & al. 2006) |
| Austria | 1853 (J. Möller, ENB): many sites |
| Belgium | 1897 (GASPAR 1966 as <i>M. laevinodis</i>) |
| Denmark | 1853 (Meinert, ZMUC): Amager |
| England | 1852 (ROEBUCK 1877 as <i>M. laevinodis</i>) |
| Finland | ≤ 1846 (NYLANDER 1846 as <i>M. laevinodis</i>) |
| France | ≤ 1855 (MAYR 1855 as <i>M. laevinodis</i>) |
| Germany | ≤ 1852 (SCHENCK 1852 as <i>M. laevinodis</i>) |
| Ireland | ≤ 1898 (CUTHBERT 1898 as <i>M. laevinodis</i>) |
| Isle of Man | ≤ 1976 (BARONI-URBANI & COLLINGWOOD 1976) |
| Italy | ≤ 1853 (MAYR 1853 as <i>M. laevinodis</i>) |
| Liechtenstein | ≤ 2004 (RADCHENKO 2004) |
| Luxembourg | ≤ 1953 (STUMPER 1953 as <i>M. laevinodis</i>) |
| Netherlands | ≤ 1887 (BOS 1887 as <i>M. laevinodis</i>) |
| Northern Ireland | ≤ 1896 (JOHNSON 1896 as <i>M. laevinodis</i>) |
| Norway | ≤ 1898 (STRAND 1898 as <i>M. levinodis</i>) |
| Portugal | ≤ 1979 (COLLINGWOOD 1979) |
| Scotland | 1825 (CURTIS 1854 as <i>M. longiscapus</i>) |
| Spain | ≤ 1879 (MARTORELL Y PEÑA 1879 as <i>M. laevinodis</i>) |
| Sweden | ≤ 1846 (NYLANDER 1846 as <i>M. laevinodis</i>) |
| Switzerland | ≤ 1855 (MAYR 1855 as <i>M. laevinodis</i>) |
| Vatican City | ≤ 1855 (MAYR 1855 as <i>M. laevinodis</i>) |
| Wales | ≤ 1913 (DONISTHORPE 1913 as <i>M. laevinodis</i>) |

It is very likely that the records from Kashmir and North India are based on misidentifications of one or more closely related *Myrmica* species found in the Himalayas (see above). The record from Turkmenistan may be a locality error based on the record of *M. laevinodis* (= *M. rubra*) in MAYR (1877) from Turkestan, a name formerly used for the region encompassing much of Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, and Uzbekistan. MENOZZI (1939) listed *M. laevinodis* (= *M. rubra*) among the 22 species of *Myrmica* known from the Himalayas and Tibet.

GLEASON (1909) listed *M. rubra* on Isle Royale, Michigan, but it seems much more likely that this record was ac-

Tab. 2: Earliest known records for *Myrmica rubra* from its native range in Central and Southeastern Europe.

| | Earliest record |
|--------------------|--|
| Bosnia/Herzegovina | ≤ 1898 (WASMANN 1898 as <i>M. laevinodis</i>) |
| Bulgaria | 1891 (FOREL 1892 as <i>M. laevinodis</i>) |
| Croatia | ≤ 1890 (KORLEVIC 1890 as <i>M. laevinodis</i>) |
| Czech Republic | ≤ 1855 (MAYR 1855 as <i>M. laevinodis</i>) |
| Greece | ≤ 1985 (AGOSTI & COLLINGWOOD 1987) |
| Hungary | ≤ 1869 (FRIVALDSZKY 1869 as <i>M. laevinodis</i>) |
| Macedonia | ≤ 1992 (PETROV & COLLINGWOOD 1992) |
| Montenegro | ≤ 1922 (KULMATYCKI 1922 as <i>M. laevinodis</i>) |
| Poland | ≤ 1855 (MAYR 1855 as <i>M. laevinodis</i>) |
| Romania | ≤ 1853 (FUSS 1853 as <i>M. laevinodis</i>) |
| Serbia | ≤ 1950 (ZIVOJINOVIC 1950 in PETROV & al. 2005) |
| Slovakia | 1907 (CSIKI 1909 as <i>M. laevinodis</i>) |
| Slovenia | ≤ 1855 (MAYR 1855 as <i>M. laevinodis</i>) |
| Turkey (European) | ≤ 1985 (AGOSTI & COLLINGWOOD 1987) |

tually some North American *Myrmica* that was considered a subspecies of *M. rubra* at the time, e.g., *M. rubra champlaini* (= *M. brevispinosa*). In 1909, virtually all records of true *M. rubra* were reported as *M. laevinodis*. CAGNIANT (1962) recorded *M. rubra* from the Atlas Mountains of Morocco. However, CAGNIANT (2006) compiled a list of ant species known from Morocco that did not include *M. rubra*, but had four other *Myrmica*. A.G.R. examined an old specimen (probably pre-1900) of *M. rubra* labeled simply "Algeria" in the ZISP collection. This record appears to fall outside the range of *M. rubra* and could be from an introduced population, intercepted in quarantine, or simply mislabeled.

For five of the questionable records, we had no specific site within the region; we mapped these as follows: Algiers in Algeria, Srinagar in Kashmir, Goose Bay in Labrador, Leh in North India, and Daşoguz in Turkmenistan.

Erroneous records: We excluded from the map the many published records of *M. rubra* from East Asia, including the Far East of Russia (ONOHAMA 1989, KUPYANSKAYA 1990, KUPYANSKAYA & LELEJ 2000, KUPYANSKAYA & al. 2000), Japan (FOREL 1901, 1907, TERANISHI 1929, EMERY 1908, 1921, ONOHAMA 1989, IMAI & al. 2003), and China (e.g., EMERY 1908, COLLINGWOOD 1962, CHANG & HE 2001, AZUMA & al. 2005), because all are almost certainly misidentifications. For example, RADCHENKO (2005) determined the East Asian *M. rubra* records in FOREL (1907), EMERY (1908, 1921), WEBER (1948), and ONOHAMA (1989) all to be *M. kotokui*.

HOLGERSEN (1943) recorded *M. rubra* (as *M. laevinodis*) from "Sajan, Sistikem, Mongolia," but Systyg Khem in

Tab. 3: Earliest known records for *Myrmica rubra* from its native range in Eastern Europe, Russia, the Caucasus, and Asia. ZMMU = Zoological Museum of the Moscow State University. + = no previously published records.

| | Earliest record |
|-----------------------|--|
| Armenia | 1900 (RUZSKY 1905 as <i>M. laevinodis</i>) |
| Azerbaijan | 1898 (RUZSKY 1905 as <i>M. laevinodis</i>) |
| Belarus | ≤ 1904 (RUZSKY 1905 as <i>M. laevinodis</i>) |
| Estonia | ≤ 1887 (MÜHLEN 1887 as <i>M. laevinodis</i>) |
| Georgia | 1899 (RUZSKY 1905 as <i>M. laevinodis</i>) |
| Kaliningrad | ≤ 1939 (JACOBSON 1939 as <i>M. laevinodis</i>) |
| Kazakhstan | 1896 (RUZSKY 1905 as <i>M. laevinodis</i>) |
| Kyrgyzstan | ≤ 1976 (TARBINSKY 1976) |
| Latvia | ≤ 1889 (NASSONOV 1889 as <i>M. laevinodis</i>) |
| Lithuania | ≤ 1889 (NASSONOV 1889 as <i>M. laevinodis</i>) |
| Moldova | ≤ 1965 (CÎRDEI & BULIMAR 1965 as <i>M. laevinodis</i> in WOJCIK & PORTER 2008) |
| Russia: Central | ≤ 1889 (NASSONOV 1889 as <i>M. laevinodis</i>) |
| + Russia: Far East | date unknown (collector unknown, ZMMU): Sakha Republic, Saldykel' |
| Russia, N. Caucasian | 1899 (Ruzsky 1905 as <i>M. laevinodis</i>) |
| Russia: North-eastern | ≤ 1889 (NASSONOV 1889 as <i>M. laevinodis</i>) |
| Russia: Siberian | ≤ 1856 (NYLANDER 1856 as <i>M. laevinodis</i>) |
| Russia: Southern | ≤ 1849 (NYLANDER 1849 as <i>M. laevinodis</i>) |
| Russia: Urals | 1894 (RUZSKY 1905 as <i>M. laevinodis</i>) |
| Russia: Volga | 1894 (RUZSKY 1905 as <i>M. laevinodis</i>) |
| Tajikistan | 1870 (MAYR 1877 as <i>M. laevinodis</i>) |
| Turkey: Kars | 1902 (RUZSKY 1905 as <i>M. laevinodis</i>) |
| Ukraine | ≤ 1892 (NASSONOV 1892 as <i>M. laevinodis</i>) |

the Sayan Mountains is actually located in Tuva, Siberia. Subsequent lists of Mongolian ant species that include *M. rubra* appear to be based on this error.

Discussion

Myrmica rubra has a very broad native distribution in Eurasia, spread over 30° of latitude and extending 8000 km across Europe and Siberia (Fig. 4). SEIFERT (1988) wrote that *M. rubra* ranged from Portugal to eastern Siberia and from Italy to northern Scandinavia, but in the Mediterranean region it was only found in moist places. RADCHENKO (2005) wrote: "*M. rubra* is a Euro-Siberian species, whose eastern limit of distribution is Lake Baikal." The present analysis largely agrees with these earlier assessments, though

Tab. 4: Earliest known records for *Myrmica rubra* from its exotic range in North America. ABS = Archbold Biological Station, MCZ = Museum of Comparative Zoology. + = no previously published records.

| | Earliest record |
|---------------------|---|
| Massachusetts | 1900 (WHEELER 1906 as <i>M. laevinodis bruesi</i>) |
| Quebec | 1915 (GRODEN & al. 2005) |
| New York | 1936 (LINDSEY 1939) |
| Maine | 1952 (GRODEN & al. 2005) |
| Rhode Island | 1966 (GRODEN & al. 2005) |
| Ontario | 1975 (GRODEN & al. 2005) |
| New Hampshire | 1977 (GRODEN & al. 2005) |
| + Washington | 1988 (M. Deyrup, ABS): Seattle |
| Nova Scotia | 1998 (GRODEN & al. 2005) |
| New Brunswick | ≤ 2005 (GRODEN & al. 2005) |
| Vermont | ≤ 2005 (GRODEN & al. 2005) |
| + Prince Edward Is. | 2008 (J.K. Wetterer, MCZ): Dalvay |

with a distribution reaching somewhat east of Lake Baikal, with one record from the Sakha Republic of the Russian Far Eastern Federal District (Tab. 3, Fig. 4). We found no *M. rubra* records from Uzbekistan and most of Kazakhstan. We believe that this gap in the distribution of *M. rubra* in Central Asia is real and not due solely to poor sampling. Almost all site records from Kazakhstan came from the mountainous regions along its northern and south-eastern borders. The arid conditions over much of Uzbekistan and Kazakhstan may exclude *M. rubra*.

DONISTHORPE (1915) noted that *M. rubra* (as *M. laevinodis*) occurs "further south in the mountains." Indeed, most of the lowest latitude records of *M. rubra* across Eurasia (39 - 42° N) were from high elevation regions in the Pyrenees, Alps, Rhodope, Caucasus, Pamir, and Tian Shan Mountains. During the last glacial maximum ~ 16,000 years ago, populations of *M. rubra* no doubt extended into much lower latitudes. But with the latest interglacial warming, populations retreated to higher latitudes or higher elevations.

In contrast to its very broad native range, *M. rubra* has a very limited distribution in North America. The few published records of *M. rubra* from Greenland, Nunavut, Labrador, and Alaska are probably based on misidentifications. The remaining *M. rubra* records in the US and Canada come from a fairly narrow band of latitude (Fig. 4), from Woods Hole, Massachusetts (41.5° N) and Newport, Rhode Island (41.5° N) in the south to Quebec City, Quebec (46.8° N) and Portage, Prince Edward Island (46.7° N) in the north. Given the enormous range of this species in the Palaearctic and how often it has been found in cargo from Europe, perhaps the most striking aspect about *M. rubra* in North America is how little it has spread over the past 100 years.

One possible explanation may be that the North American populations of *M. rubra* have a fairly narrow range of climatic tolerances. In Europe, different *M. rubra* populations show physiological adaptations to the local climate (ELMES & al. 1999). Thus, although the species as a whole is able to live under a great diversity of climatic conditions in Europe and Asia, any one population has a much narrower tolerance range. It is possible that the populations of *M. rubra* now in North America are descended from colonists from a narrow geographic area or even a single locale and are not adapted to spread much beyond their current latitudinal range in the New World. Most *M. rubra* records in North America are from the past ten years, suggesting that the North American populations are expanding. While it is not clear what the latitudinal limits are, there appears to be no geographic barriers that would prevent *M. rubra* from spreading across the US and Canada from the Atlantic to Pacific coasts.

Impact: In addition to its sting, *M. rubra* may become a crop pest through tending plant-feeding aphids. SEIFERT (1988) wrote that *M. rubra* "tends aphids more frequently than other members of the genus." In some areas (e.g., along rivers and streams in Carpathian Mountains), *M. rubra* forms huge supercolonies consisting of hundreds of interconnected nests with hundred of thousands (or even millions) of workers. In these areas, population densities of *M. rubra* may become very high (A.G. Radchenko, unpubl.). STURTEVANT (1931) wrote of *M. laevinodis bruesi* (= *M. rubra*) in Woods Hole, Massachusetts, where *M. rubra* was first found in 1900: "This form was described from specimens taken in the woods adjoining the Fay Rose Gardens. It is now the dominant ant in these woods, but I have been unable to find a single specimen in any other place. The numerous nests seem to represent branches of a single family, since transfers of workers never lead to fighting in spite of the fact that the species is very pugnacious and has the most painful sting of any ant I have encountered in the northeastern states." GARNAS & al. (2007), however, did not find large-scale supercolonies in the *M. rubra* populations of Maine.

In the native range of *M. rubra*, a complex of co-evolved competitors and natural enemies may keep most *M. rubra* populations in check. For example, SEIFERT (1988) wrote that *M. rubra* and *M. ruginodis* "have a high ecological similarity or overlap of their fundamental niches (63%) but their real habitat overlap is 12.9% only ... which indicates a strong competitive displacement."

In North America, the absence of co-evolved competitors and natural enemies may allow *M. rubra* populations to expand to levels where they become significant pests. Reports of *M. rubra* as a serious pest in North America are all recent. SPIERING (2009) wrote that at the Tiff Nature Preserve in Buffalo, New York, *M. rubra* "were discovered on the preserve in the mid-1980's and soon became such a serious pest that sections of the preserve needed to be closed to the public at times." The earliest record of *M. rubra* from New Brunswick dates to 1998, but now reports of this species as a pest come from all over the province (TOAL 2008). Recently there have been enormous outbreaks of *M. rubra* in coastal Maine, particularly on Mount Desert Island (GRODEN & al. 2005).

Why is *M. rubra* suddenly emerging as a pest after more than a century of residence? One possibility is that a new

strain of *M. rubra* has been recently introduced to North America. If the *M. rubra* population found in Woods Hole, Massachusetts in 1900 still persists, it would be interesting to examine whether or not it genetically matches populations in other parts of North America. In any event, it seems likely that if *M. rubra* populations in North America continue expanding, this species will become a familiar stinging pest ant in temperate North America.

Acknowledgements

We thank M. Wetterer and A. Wetterer for comments on this manuscript; S. Cover (MCZ) and M. Deyrup (ABS) for help with their respective ant collections; H. Zettel, S. Tschesnokova, R. Schultz, J. Huber, A. Francoeur, G. Elmes, and M. Bustos for supplying unpublished records; W. O'Brien for GIS help; D.P. Wojcik and S.D. Porter for compiling their valuable FORMIS bibliography; R. Pasos and W. Howerton of the FAU library for processing so many interlibrary loans; and Florida Atlantic University for financial support.

Zusammenfassung

Die Ameise *Myrmica rubra* (LINNAEUS, 1758) (früher *Myrmica laevinodis* NYLANDER, 1846) ist eine aggressive eurasische Art mit mächtigem Stich, die sich derzeit im temperaten Nordamerika ausbreitet. Hier wird der Trivialname "ruby ant" vorgeschlagen. Um die weltweite Verbreitung von *M. rubra* zu dokumentieren und ihr Potenzial zur weiteren Ausbreitung abzuschätzen, haben wir veröffentlichte und unveröffentlichte Nachweise von > 2000 Fundorten zusammengetragen. Wir berichten von den frühesten bekannten Nachweisen der Art für 71 geographische Gebiete (Länder, große Inseln, US-Bundesstaaten, kanadische Provinzen und russische Föderationskreise), einschließlich dreier Gebiete ohne bisher veröffentlichte Nachweise: Prince Edward Island, der Staat Washington und der russische Föderationskreis Ferner Osten. Bei allen veröffentlichten Nachweisen von *M. rubra* aus Ostasien, einschließlich Japans, Chinas und des östlichsten Teils Russlands, scheint es sich um Fehlbestimmungen von *Myrmica kotokui* FOREL, 1911 zu handeln.

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