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Geographic spread of *Vollenhovia emeryi* (Hymenoptera: Formicidae)

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ABSTRACT. *Vollenhovia emeryi* Wheeler is a small and inconspicuous ant species originally from East Asia that recently has been found in North America. Here, we examine the geographic spread of *V. emeryi* and compare its native range in Asia with its exotic range in North America. We compiled published and unpublished *V. emeryi* specimen records from >300 sites. We documented the earliest known *V. emeryi* records for 14 geographic areas, ten in Asia (Japan, North Korea, South Korea, Taiwan, Thailand, and five provinces of China) and four in North America (Maryland, Pennsylvania, Virginia, and Washington DC). Reports of *V. emeryi* from lower latitude (14.3°N to 25.1°N) sites in Taiwan, Thailand, and southern China, however, probably represent a distinct species. *Vollenhovia emeryi* has a much broader latitudinal spread in East Asia (at least 13.5° range: 29.7°N to 43.2°N) than it has in North America (1.3° range: 38.7°N to 40.0°N). The North American records of *V. emeryi* are all at latitudes near the northernmost records in Asia. It seems likely that *V. emeryi* will spread further in North America, particularly towards the south and west.

Keywords: biogeography, biological invasion, exotic species, invasive species

INTRODUCTION

Forel (1911) compiled a list of tramp ant species, spread by human commerce, which had achieved or were in the process of achieving broad cosmopolitan distributions. The 14 cosmopolitan species on this list all originated in the tropics and/or subtropics. However, in what appears be a new trend, several temperate ant species are spreading outside their native hemisphere (e.g., *Myrmica rubra* (L.); Wetterer & Radchenko 2011), including five ant species native to temperate East Asia that are now spreading in temperate North America (earliest North American record in parentheses): *Brachyponera chinensis* (Emery) (1932; Guénard & Dunn 2010), *Nylanderia flavipes* (Smith) (1939; Wetterer 2011), *Vollenhovia emeryi* Wheeler (1986; Kjar & Suman 2007), *Strumigenys hexamera* (Brown) (1987; MacGown & Wetterer 2012), and *Tetramorium tsushimae* Emery (1988; Reuther 2009). Here, we examine the geographic distribution of *V. emeryi* and compare its native range in Asia with its exotic range in North America.

Wheeler (1906) described *V. emeryi* from Japan. Radchenko (2005) designated *Vollenhovia emeryi chosenica* Wheeler, described from South Korea, as a junior synonym of *V. emeryi*.

Vollenhovia emeryi colonies typically nest in the wood and under the bark of fallen trees (Terayama & Yamauchi 2003; BG, pers. obs.) in old-growth and second-growth deciduous and conifer forests (Japan Ant Database Group 2003, Maeto & Sato 2004, Kwon et al. 2005, Hosoishi et al. 2007). This species is also occasionally found in urban parks (Iwata et al. 2005, Harada et al. 2010) and in agricultural fields (Hosoishi et al. 2007).

Much recent research on *V. emeryi* concerns their remarkable mode of reproduction. *Vollenhovia emeryi* queens produce daughter queens through parthenogenesis and produce males that are clones of their mates (Ohkawara et al. 2006; Kobayashi et al. 2008, 2011, 2012), a reproductive mode similar to that reported for some other ant species, including the tramp ants *Wasmannia auropunctata* (Roger) and *Paratrechina longicornis* (Latr.) (Fournier et al. 2005; Pearcy et al. 2011), but with some additional complexity. Whereas *V. emeryi* workers are monomorphic (Fig. 1), *V. emeryi* queens have two morphotypes: long-winged (L) and short-winged (S) (Figs. 2-3). Males also occur in two genetically discrete (but morphologically indistinguishable) types, with L and S males mating only with L and S queens, respectively (Kobayashi et al. 2011). The queen and male genomes do not mix in reproductives and there is no recent gene flow between queens and males (Kobayashi et al. 2011). Phylogenetically, S morph queens form their own clade, whereas the L morph queens are paraphyletic, indicating the L morph is the primitive condition (Kobayashi et al. 2012). Thus, the S morph *V. emeryi* would seem in most ways like a separate species from the L morph *V. emeryi*, except for one twist: S males appear to be more closely related to L queens and L males than they are to S queens (Kobayashi et al. 2008).

METHODS

Using published and unpublished records, we documented the worldwide range of *V. emeryi*. We obtained unpublished site records from museum specimens in the collections of the Museum of Comparative Zoology (MCZ, identified by S. Cover) and the Smithsonian Institution (SI, identified by M. Smith). In addition, we used on-line databases with collection information on

Table 1. Earliest known records for *Vollenhovia emeryi*. * = may be based on misidentifications (see text)

Asia	**Earliest record**
Japan	1905 (Wheeler 1906)
Taiwan	1908 (Forel 1912)
South Korea	≤1928 (Wheeler 1928 as *V. emeryi chosenica*)
North Korea	1970 (Radchenko 2005)
Thailand*	1981 (Brown 1988)
Yunnan, China*	≤1999 (Xu et al. 1999)
Zhejiang, China*	≤2001 (Zhou 2001)
Guangxi, China*	≤2001 (Zhou 2001)
Hunan, China*	≤2005 (Huang & al. 2005)
Hubei, China*	≤2009 (Wang & Zhao 2009)

North America	**Earliest record**
Washington DC	1986 (Kjar & Suman 2007)
Pennsylvania	1993 (King & Green 1993)
Virginia	2002 (Kjar & Suman 2007)
Maryland	2003 (Kjar & Suman 2007)

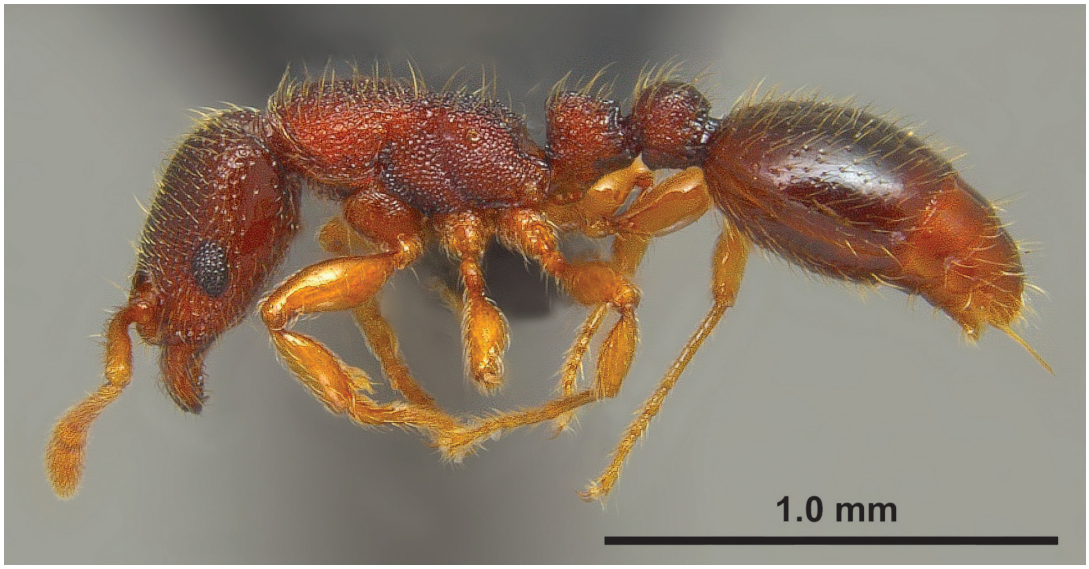

Fig. 1. *Vollenhovia emeryi* worker from Cabin John Regional Park, Maryland (photo by Joe MacGown from www.antweb.org).

Fig. 2. *Vollenhovia emeryi* long-winged queen from Rock Creek Regional Park, Maryland (photo by Joe MacGown from www.antweb.org).

specimens by Antweb (www.antweb.org), the Global Biodiversity Information Facility (www.gbif.org), and the Japanese ant image database (Terayama & Yamauchi 2003).

We obtained geo-coordinates for collection sites from published references, specimen labels, maps, or geography web sites (e.g., earth.google.com and www.tageo.com). If a site record listed a geographic region rather than a "point locale," and we had no other record for this region, we used the coordinates of the capital or largest town of the region or, in the case of small islands and natural areas, the center of the region.

We did not map records of *V. emeryi* found in newly imported goods or intercepted in transit by quarantine inspectors at a port of entry because the original source of such material is never known. For example, in 1961, *V. emeryi* was intercepted in Hawaii in a shipment of pine from Japan (antweb.org).

Radchenko (2005) determined that specimens from North Korea that Collingwood (1976) identified as *Leptothorax congruus* Smith were actually *V. emeryi*. We assumed Forel's (1912) record of *V. emeryi* from Pilam (now Beinan), Taiwan was based on the specimen that T. Shiraki collected in 1908 at Pilam (Taiwan Agricultural Research Institute; http://digiins.tari.gov.tw/tarie/search_Result2E.php?id=form08159001).

RESULTS AND DISCUSSION

We compiled published and unpublished *V. emeryi* specimen records from >300 sites (Fig. 4). We documented the earliest known *V. emeryi* records for 14 geographic areas: ten in Asia (Japan, North Korea, South Korea, Taiwan, Thailand, and five provinces of China) and four in North America (Maryland, Pennsylvania, Virginia, and Washington DC) (Table 1). Records ranged from sea level (Ogata et al. 1994) to 1450 m elevation (Kwon et al 2014).

At the northern end of the Asian range, we found only seven records of *V. emeryi* at latitudes higher than 40.0°N: five from Japan (up to 43.2°N in Hokkaido; Morisita 1945, Hayashida 1957, 1961, Terayama 1994) and two from North Korea (up to 41.8°N; Radchenko 2005). Terayama & Kinomura (1997) wrote that *V. emeryi* "is commonly and widely distributed from Hokkaido to Yaku-shima." We found only two records of *V. emeryi* in Japan south of Yaku-shima, i.e., from Nakano-shima (29.9°N; Harada et al. 2014) and Taira-jima (29.7°N; Ogata 1981). However, we found records from much lower latitudes in other parts of Asia, i.e., in Thailand (14.3°N; Brown 1988), Taiwan (22.8°N & 25.1°N; see Results), and southern China (Xishuangbanna, Yunnan Province: 22.0°N, Xu et al. 1999; Guangxi Province: ~22.8°N, Zhou 2001).

The absence of *V. emeryi* from the many Japanese islands south of Taira-jima combined with the great latitudinal difference between Taira-jima and the records from much lower latitudes in Thailand, Taiwan, and China suggests that the latter records may be based on misidentifications. In fact, Terayama (2009) explicitly excluded *V. emeryi* from the list of ants of Taiwan, writing: "although Forel (1912) recorded *V. emeryi* from Pilam (= Taitung Pref.), no reliable additional record is known." Forel's (1912) '*V. emeryi*' specimens from Taiwan may be the same species as *Vollenhovia* cf. *emeryi* reported by Fellowes et al. (2002, 2003) from southern China (Hainan Island: 18.8°N; Guangxi Province: 23.7°N). In fact, it is possible that the more temperate records of *V. emeryi* from China (Hubei Province: ~30.6°N, Wang & Zhao 2009; Zhejiang Province: 29.0°N, Zhou 2001; Hunan Province: 25.3-29.7°N, Huang et al. 2005) are also based on misidentifications. Morphological and genetic evaluation of putative *V. emeryi* specimens from China, Taiwan, and Thailand would be valuable in establishing the geographic and taxonomic limits of *V. emeryi*.

In 1986, Stefan P. Cover discovered the first North American population of *V. emeryi* in Rock Creek Park, Washington DC. Since then, additional North American populations have been reported from Maryland, Pennsylvania, and Virginia (Table 1; Fig. 4). Overall, *V. emeryi* records ranged (north to south) from Philadelphia, Pennsylvania (40.0°N; King & Green 1993) to Fort Washington Park, Maryland (38.7°N; Kjar & Suman 2007). Thus, *V. emeryi* has a ten times broader latitudinal spread in Asia (at least 13.5° range: 29.7°N to 43.2°N) than it has in North America (1.3° range: 38.7°N to 40.0°N). The North American records of *V. emeryi* are all from latitudes near the northernmost records in Asia (Fig. 4). One possible explanation for this pattern may be that the North American populations of *V. emeryi* have a fairly narrow range of temperate climatic tolerances. In Asia, different *V. emeryi* populations may show physiological adaptations to the local climate. Thus, although the species as a whole is able to live under a great diversity of climatic conditions in Asia, any one population has a much narrower tolerance range. It is possible that the populations of *V. emeryi* now in North America are descended from colonists from a narrow geographic area and are not

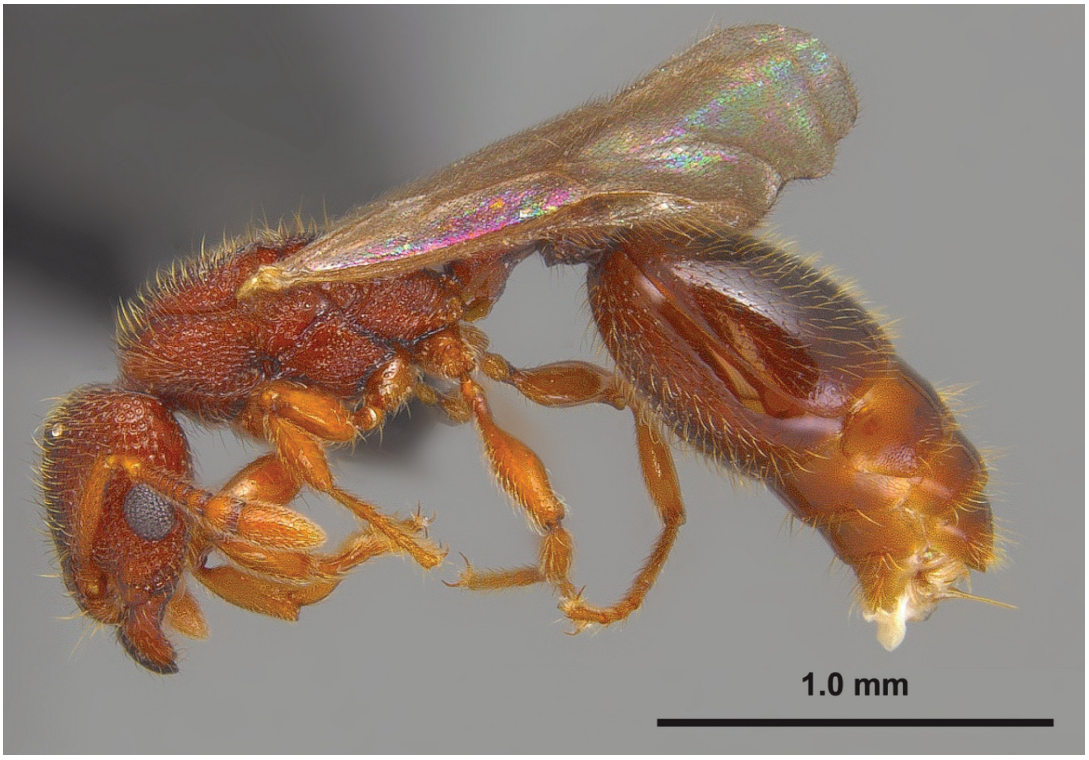

Fig. 3. *Vollenhovia emeryi* short-winged queen from Cabin John Regional Park, Maryland (photo by Joe MacGown from www.antweb.org).

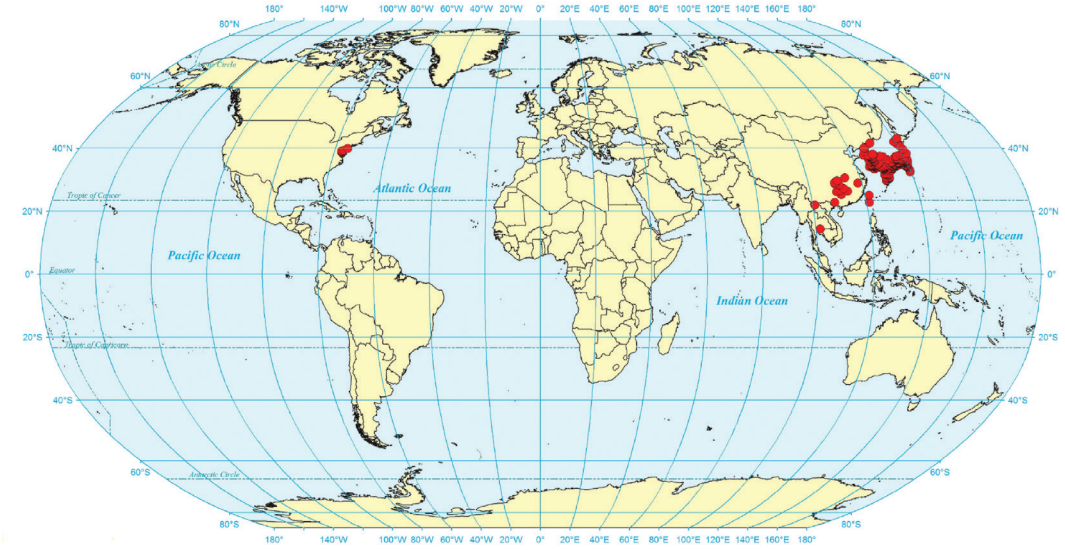

Fig. 4. Worldwide distribution records of *Vollenhovia emeryi.* Records from Taiwan, Thailand, and China may be based on misidentifications (see text).

adapted to spread much beyond their current latitudinal range. While it is not clear what its potential latitudinal limits are in North America, there appears to be no geographic barriers that would prevent *V. emeryi* in North America from spreading towards the north, south, and west. The micro-satellite markers of *V. emeryi* specimens from North America do not match the micro-satellite markers of any Asian population that has been examined so far (D.B. Booher, unpublished data, M. Okamoto, pers. comm.), thus the geographic origins of the exotic North American populations remain unknown.

Kjar & Suman (2007) reported that all *V. emeryi* queens found in North America were S morph. The L morph queens and males typically mate during nuptial flights, whereas the S morph queens and males mate primarily with siblings within their natal colonies (Okamoto & Ohkawara 2010). Kjar & Suman (2007) speculated that any long-range dispersal would be limited in North America because S morph *V. emeryi* do not have nuptial flights. In 2012, however, D. Booher & R.M. Duffield collected long-winged *V. emeryi* queens for the first time in North America (Fig. 2), though preliminary genetic analyses indicate these may be atavistic S morph queens (D.B. Booher, unpublished data).

Booher & Duffield (pers. obs.) found that *V. emeryi* has become the most common litter dwelling ant at some sites in Rock Creek Regional Park and in some riparian forests bordering the Chesapeake & Ohio Canal in Maryland. Thus, if *V. emeryi* does become more widespread in North America, it is possible that this species could have significant ecological impacts in its exotic range.

Kinomura & Yamauchi (1992) described *Vollenhovia nipponica* Kinomura & Yamauchi, a workerless social parasite that lives in the nests of *V. emeryi*. In Asia, *V. nipponica* is now known from eight prefectures in Japan with a latitudinal range of 31.4°N to 36.6°N (Terayama and Yamauchi 2003), all further south than the known range of *V. emeryi* in North America. In 2012, D. Booher & R.M. Duffield collected *V. nipponica* for the first time in North America, at Rock Creek Regional Park, Maryland. So far, *V. nipponica* are only known to parasitize colonies of S morph *V. emeryi.* Genetic analyses of native and exotic populations of *V. nipponica* and their host *V. emeryi* colonies should prove to be valuable in untangling the complicated genetic and ecological relations of *V. nipponica* and *V. emeryi.*

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