Review of the ant genus *Manica* (Hymenoptera, Formicidae), with a new record of the genus in China and description of a new species

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Abstract

Seven known extant species of *Manica* have been identified worldwide: *M. bradleyi* (Wheeler, 1909), *M. hunteri* (Wheeler, 1914), *M. invidia* Bolton, 1995, *M. parasitica* (Creighton, 1934), *M. rubida* (Latreille, 1802), *M. shanyii* sp. nov., and *M. yessensis* Azuma, 1955. The discovery of the new species is documented from Sichuan Province, China, marking the first recorded instance of the genus *Manica* in China. Additionally, an identification key for distinguishing the known species within the genus *Manica* is provided.

Keywords

Distribution map, *Manica shanyii* sp. nov., Myrmicinae, Myrmicini, taxonomy

Introduction

The genus *Manica*, first described by Jurine in 1807, traces its origins to at least the Eocene epoch (Zharkov et al. 2023). Presently, *Manica* stands out as a rare genus in ants, classified within the tribe Myrmicini of the subfamily Myrmicinae. However, the morphological definition of the tribe Myrmicini has been challenging due to a lack of distinctive characteristics (Jansen and Savolainen 2010). Initially, Myrmicini was defined based on several morphological features, many of which were not exclusive to
Myrmicini, encompassing seven genera (Bolton 2003). Recent molecular studies have suggested that the tribe may not be monophyletic (Brady et al. 2006; Moreau et al. 2006), although there were discrepancies regarding the genera included in the tribe. It was only later, with the work conducted by Ward et al. (2015), that the membership of Myrmicini was restricted to two genera, *Manica* and *Myrmica*, establishing its position as sister to all other members of the subfamily.

Currently, only six extant species and two fossil species of *Manica* are recognized in the Holarctic region. Among these, *M. rubida* (Latreille, 1802) is distributed in Europe (Borowiec 2014); while four species, namely, *M. bradleyi* (Wheeler, 1909), *M. hunteri* (Wheeler, 1914), *M. invidia* Bolton, 1995 and *M. parasitica* (Creighton, 1934), are found in western North American. *Manica yessensis* Azuma, 1955 is endemic to Japan, representing the sole recorded species of *Manica* in Asia so far. Despite extensive surveys in the region, no additional species of this genus have been discovered in the past 70 years. However, given the extant distribution of this genus in Japan and southern Europe, with China's vast expanse offering numerous habitats suitable for *Manica*, it is plausible that cryptic, undiscovered species of *Manica* may exist in China.

In this study, while examining ants from the Emei and Gongga Mountains in Sichuan Province, China, we identified a new species of the genus *Manica*, marking the first documented occurrence of the genus and a new species in China. Here, we describe this new species and recognize the six known extant species, providing an identification key to *Manica* species based on the worker caste.

**Materials and methods**

The specimens of *Manica shanyii* sp. nov. were collected alive during field expeditions to Emei and Gongga Mountains in Sichuan, China (Fig. 1) by hand. Subsequently, they were preserved in a vial containing absolute ethyl alcohol. The specimens were then pin-mounted and examined using a Leica M205A stereomicroscope. High-quality multifocused montage images were generated with a KEYENCE (VHX-6000) digital imaging system.

The images of the *Manica* species, accessible on AntWeb (https://www.antweb.org), were meticulously examined and compared. The general terminology for *Manica* workers adheres to Bolton (1975). All measurements are given in millimeters. The abbreviations employed for the measurements and indices are as follows:

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tbody>
<tr>
<td>CI</td>
<td>Cephalic Index = HW × 100 / HL.</td>
</tr>
<tr>
<td>DPI</td>
<td>Dorsal Petiole Index = DPW × 100 / PL.</td>
</tr>
<tr>
<td>DPW</td>
<td>Dorsal Petiole Width, maximum width of petiole in dorsal view.</td>
</tr>
<tr>
<td>ED</td>
<td>Eye Diameter, maximum diameter of eye.</td>
</tr>
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| HL           | Head Length, straight-line length of head in full-face view, measured from midpoint of anterior clypeal margin to midpoint of posterior
margin, or terminal horizontal line in some species with a concave posterior margin.

- **HW**: Head Width, maximum width of head in full-face view, excluding eyes.
- **LPI**: Lateral Petiole Index = PH × 100 / PL.
- **MSL**: Mesosoma Length, diagonal length of mesosoma in lateral view, measured from point at which pronotum meets cervical shield to posterior basal angle of metapleuron.
- **PH**: Petiole Height, height of petiole measured in lateral view from apex of ventral (subpetiolar) process vertically to a line intersecting dorsal most point of node.
- **PL**: Petiole Length, length of petiole measured in lateral view from anterior process to posterior most point of tergite, where it surrounds gastral articulation.
- **PW**: Pronotal Width, maximum width of pronotum measured in dorsal view.
- **SI**: Scape Index = SL × 100 / HW.
- **SL**: Scape Length, straight-line length of antennal scape, excluding basal constriction or neck.
- **TL**: Total Length, total outstretched length of individual, from mandibular (occlusion) apex to gastral apex (not including the sting).

The holotype and paratypes specimens have been or will be deposited in the following institutions:

- **GXNU**: Insect Collection, Guangxi Normal University, Guilin, Guangxi, China.
- **IZCAS**: Institute of Zoology, Chinese Academy of Sciences, Beijing, China.

**Figure 1.** Global map showing the type localities of †*M. andranmae*, †*M. bradleyi*, †*M. hunteri*, †*M. invidia*, †*M. iviei*, †*M. parasitica*, †*M. rubida*, †*M. shanyii* sp. nov. and †*M. yessensis* (Source: Esri, Maxar, GeoEye, Earthstar geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community).
Results

Synopsis of Manica species

†M. andrannae Zharkov & Dubovikoff, 2023 [Baltic Amber]
M. bradleyi (Wheeler, 1909) [United States]
M. hunteri (Wheeler, 1914) [Canada, United States]
M. invidia Bolton, 1995 [Canada, United States]
M. parasitica (Creighton, 1934) [United States]
M. rubida (Latreille, 1802) [Andorra, Armenia, Austria, Belgium, Bulgaria, Croatia, Czech Republic, France (type locality), Georgia, Germany, Greece, Hungary, Italy, Montenegro, Poland, North Macedonia, Romania, Slovakia, Slovenia, Switzerland, Turkey]
†M. iviei LaPolla, 2023 [United States]
M. shanyii sp. nov. [China]
M. yessensis Azuma, 1955 [Japan]

Key to Manica based on worker castes

1 Posterior portion of the head and dorsum of mesosoma smooth and shining, (Fig. 5) [United States]................................. M. parasitica (Creighton, 1934)
   – Posterior portion of the head and dorsum of mesosoma more or less striate or punctate (Figs 2, 4) ................................................................. 2

2 Body uniformly colored, ranging from brownish yellow, reddish brown to blackish (Figs 3, 4, 7) ................................................................. 3
   – Body bicolored, head and gaster black with mesosoma, petiole and postpetiole reddish brown (Figs 2, 8), or gaster blackish brown with head, mesosoma, petiole and postpetiole yellowish brown (Fig. 6) ........................................ 5

3 Dorsum of pronotum and mesonotum abundantly transversely striate (Fig. 7B) [China] ................................................................. M. shanyii sp. nov.
   – Dorsum of pronotum and mesonotum longitudinally rugose (Figs 3C, 6C, 8C) ................................................................. 4

4 In lateral view, lateral face of mesosoma, petiole, and postpetiole mainly punctate, appearing dull and not shining (Fig. 4D); in lateral view, postpetiole as long as high (Fig. 4D) [Canada, United States] ................................................................. M. invidia Bolton, 1995
   – In lateral view, lateral face of mesosoma longitudinally striate and without punctae, petiole and postpetiole smooth and shining (Fig. 3D); in lateral view, postpetiole compressed anteroposteriorly, distinctly higher than long (Fig. 3D) [Canada, United States] ............................. M. hunteri (Wheeler, 1914)

5 Head reddish brown (Fig. 6A); dorsum of pronotum only with indistinctly, finely longitudinal striation, extremely shining (Fig. 6C); in lateral view, the
posterior face of postpetiole straight and steep (Fig. 6D) [Western Europe].

\[M. \text{rubida (Latreille, 1802)}\]

- Head black (Figs 2A, 8A); dorsum of pronotum with prominent rugae and not shining (Figs 2C, 8C); in lateral view, the posterior face of postpetiole unconspicuous (Fig. 2D) or sloping forward (Fig. 8D).

\[M. \text{bradleyi (Wheeler, 1909)}\]

- In lateral view, anteroventral corner of postpetiole distinctly conically protuberant (Fig. 2D); dorsal face of postpetiole evenly and slightly convex (Fig. 2D); petiole and postpetiole smooth and shining (Fig. 2C, D) [United States].

\[M. \text{yessensis Azuma, 1955}\]

**Taxonomic accounts of Manica**

*Manica bradleyi* (Wheeler, 1909)


**Type material.** Unexamined, but high-resolution images of syntype worker (CASENT0907664, imaged by Alexandra Westrich) were reviewed.

**Diagnosis.** Head and gaster blackish brown to black, while mesosoma yellow. In lateral view, postpetiole as broad as its long, with an evenly convex anterior margin and a unconspicuous posterior margin; ventral surface flat, lacking any pointed protuberance. Petiole and postpetiole smooth and shining.

**Recognition.** *M. bradleyi* (Wheeler, 1909) and *M. yessensis* Azuma, 1955, are easily distinguishable from all other species of Manica due to their distinctive characteristics. They both feature a black or dark brown head and gaster, contrasted with a light brown to reddish yellow mesosoma. Furthermore, *M. bradleyi* can be easily identified from *M. yessensis* by its postpetiole, which is as long as its high in lateral view, with a distinctly conically protuberant anteroventral corner; the dorsal face of the postpetiole is evenly and slightly convex, while both the petiole and postpetiole exhibit a smooth and shining appearance (Fig. 2C, D).

**Distribution.** In the Sierra Nevada Mountains of California, western Nevada, and the Transverse Ranges in southern California, with a single record from the Cascade Range of Oregon.
**Manica hunteri** (Wheeler, 1914)

Fig. 3


**Type material.** Unexamined, but high-resolution images of worker specimen were reviewed from AntWeb (CASENT0922741, imaged by Wade Lee, label’s photo by Michele Esposito).

**Diagnosis.** Body uniformly brownish yellow. In lateral view, dorsum feebly convex, with posterolateral corner of propodeum obtusely angular. Additionally, in lateral view, postpetiole compressed anteroposteriorly, distinctly higher than long. The lateral face of mesosoma longitudinal striae without puncta, while petiole and postpetiole smooth and not shining.

**Recognition.** *M. hunteri* (Wheeler, 1914) and *M. invidia* Bolton, 1995 can be easily distinguished from the congeners of this genus by their uniformly brownish yellow, or reddish brown to blackish. While *M. hunteri* may initially resemble an immature *M. invidia*, closer examination reveals distinct characteristics that differentiate them. In lateral view, the postpetiole of *M. hunteri* compressed anteroposteriorly, distinctly higher than long. Additionally, the lateral face of mesosoma exhibits longitudinal striae without puncta, and both petiole and postpetiole are smooth and shining (Fig. 3D).

**Distribution.** From northern Utah and northern Nevada to central California, extending northwards into southern Canada. The northernmost is Edmonton, Alberta, while the easternmost range extends to Sundance, Wyoming.

**Manica invidia** Bolton, 1995

Fig. 4


**Type material.** Unexamined, but high-resolution images of syntype worker (CASENT0904061, imaged by Alexandra Westrich) were reviewed.

**Diagnosis.** Body dully yellow or nearly orange. In lateral view, posterolateral corner of propodeum broadly rounded. Furthermore, in lateral view, postpetiole as long as
high. The lateral face of mesosoma, petiole, and postpetiole mainly punctate, appeared dull and not shining.

**Recognition.** *M. invidia* Bolton, 1995 bears resemblance to *M. hunteri* (Wheeler, 1914), yet it can be distinguished by the following characteristics: in lateral view, the

![Figure 2](https://www.antweb.org/CASENT0907664)

*Manica bradleyi* worker (Syntype, images cited from [https://www.antweb.org/](https://www.antweb.org/), imaged by Alexandra Westrich) **A** head in full-face view **B** label **C** body in dorsal view **D** body in lateral view.
Figure 3. Manica hunteri worker (Non-type, images cited from https://www.antweb.org/, CASENT0922741, specimen's photos by Wade Lee, label's photo by Michele Esposito) **A** head in full-face view **B** label **C** body in dorsal view **D** body in lateral view.
Figure 4. *Manica invidia* worker (Syntype, images cited from https://www.antweb.org/, CASENT0904061, imaged by Alexandra Westrich) **A** head in full-face view **B** label **C** body in dorsal view **D** body in lateral view.
mesosoma, petiole, and postpetiole are predominantly punctate, resulting in a dull and non-shining appearance (Fig. 4D); the posterolateral corner of propodeum in lateral view broadly rounded; and the postpetiole is as long as its high.

**Distribution.** From the eastern slopes of the Sierra Nevada and the Cascade Range in California, eastward to northeastern New Mexico, Colorado, Wyoming, the Black Hills of South Dakota and southwestern North Dakota, northwestward into British Columbia and Alberta, with one record from Alaska.

Manica parasitica (Creighton, 1934)

Fig. 5


**Type material.** Unexamined, but high-resolution images of syntype worker (CASENT0005974, imaged by April Nobile) were reviewed.

**Diagnosis.** Body almost uniformly light blackish brown. Head smooth and shining, except for the frontal area and cheek with longitudinal stripes. Similarly, mesosoma and metasoma smooth and shining, except for katepisternum and the lower part of lateral face of propodeum with finely punctate-striate patterns.

**Recognition.** *M. parasitica* (Creighton, 1934) can be easily distinguished from the congeners of this genus by the characteristics mentioned in the “Diagnosis” of this species.

**Distribution.** This species is only known from a few records in the Sierra Nevada Mountains in California.

Manica rubida (Latreille, 1802)

Fig. 6

Formica rubida Latreille, 1802: 267, pl. 10, fig. 65 (q.) FRANCE. Combination in Manica by Jurine, 1807: 279; in Myrmica by Schenck, 1852: 132; in Myrmica (Oreomyrma) by Wheeler 1914: 118; in Myrmica (Neomyrma) by Emery, 1915: 69 (footnote), Forel, 1915: 364; in Neomyrma by Bondroit, 1918: 97; in Myrmica (Manica) by Emery, 1921: 43; in Manica by Weber, 1947: 440. Myrmica leonina Losana, 1834: 332, pl. 36, fig. 7 (w.) ITALY. Synonymized by Roger, 1859: 252. Myrmica montana Labram & Imhoff, 1838, pl. 36, figs 1–3 (w.q.m.) SWITZERLAND. Synonymized by Roger, 1859: 252.

**Type material.** Unexamined, non-type worker, but high-resolution images of worker specimen were reviewed from AntWeb (CASENT0173135, specimen’s photos by April Nobile, label’s photo by Michele Esposito).
Diagnosis. Body reddish brown with gaster blackish brown. In lateral view, with posterolateral corner of propodeum obtusely angular. Petiole node in lateral view with an almost vertical posterior face. Postpetiolar node in lateral view with a vertical posterior face; postpetiolar sternite anteroventrally produced as an acute angle directed forward.
Recognition. *M. rubida* (Latreille, 1802) can be easily distinguished from the congener of this genus by the following characteristics: the body is reddish-brown with a gaster that is distinctly darker than the reddish-brown head. Additionally, in lateral view, the petiolar node is erect, exhibiting distinct anterior and posterior margins along...
with a well-defined dorsal margin. Similarly, the postpetiolar node, when viewed laterally, displays a vertical posterior face.

**Distribution.** This species is found in the mountainous regions of Central and Southern Europe (excluding the Iberian Peninsula), Ukraine (including Crimea), Turkey, and the Caucasus.

__Manica shanyii sp. nov.__
https://zoobank.org/F7ECF81C-86B9-4F92-8BA2-CE8186F6FFBC

Fig. 7

**Type material.** Holotype worker, CHINA, Sichuan, Leshan City, Lei Dongping of Emei Mountain, 29.5252°N, 102.3320°E, 2900 m, 2. Aug. 2011, leg. Ruigang Yang, No. GXNU110273; 3 paratype workers, CHINA, Sichuan, Garze Tibetan Autonomous Prefecture, Moxi Town, Hailuogou in the Gongga Mountain National Nature Reserve, 29.5845°N, 102.0289°E, 2740 m, 28. May. 2022, leg. Yanping Wu, No. GXNU220539. [Holotype worker and two paratype worker are deposited in the Insect Collection of Guangxi Normal University, Guilin, Guangxi, China (GXNU), one paratype worker are deposited in Institute of Zoology, Chinese Academy of Sciences, Beijing, China (IZCAS)].

**Diagnosis.** Body brownish black. In full-face view, head longer than broad, with broadly rounded posterior corners; the anterior margin of clypeus narrowly rounded, without prominent botches medially; the antennal scapes slightly surpass the posterior corners of the head. In lateral view, the dorsum of propodeum roughly straight, with obtusely angular posterolateral corners. Petiole in lateral view slightly longer than high, with a slightly concave anterior margin and a dorsal outline more or less narrowly rounded; the subpetiolar process in lateral view acutely toothed anteroventrally. Similarly, the postpetiole in lateral view as broad as long, with a convex anterior margin and steep posterior margin; the sternite slightly convex, with rounded anteroinferior corners.

**Holotype worker.** TL 6.32, HL 1.64, HW 1.45, CI 87.96, SL 1.31, SI 90.46, ED 0.34, PW 0.99, MSL 2.241, PL 0.61, PH 0.46, DPW 0.39, LPI 75.21, DPI 64.20.

**Description.** **Head.** In full-face view, the head longer than broad, with slightly convex lateral margins and broadly rounded posterior corners, while the posterior margin nearly straight (Fig. 7A). Mandibles slightly convex and armed with one large apical tooth, one secondary tooth, and followed by five smaller teeth. The anterior margin of clypeus relatively narrowly rounded, with a prominent upward edge in the middle. Frontal carinae curved outwards to merge with the rugae surrounding the antennal sockets, but they not reaching to middle of head (Fig. 7A). Frons wide, frontal lobes not extended. Antennae 12-segmented, featuring with a distinct 5-segmented club; scape relatively long, slightly surpassing the posterior corners of the head, and gradually curved at the base, without any trace of lobe or carina (Fig. 7A). Ocelli absent. Eyes relatively large, located slightly before the mid-point of the lateral sides of the head (Fig. 7A). **Mesosoma.** In lateral view, promesonotum evenly convex; metanotal groove strongly depressed; propodeum roughly straight, passing through a distinct, but obtuse
angle or obtuse roundness into the somewhat straight and sloping declivity (Fig. 7C). In dorsal view, rather robust, with a faint but visible promesonotal suture; lateral margins slightly convex, anterior margin convex, and posterior margin slightly concave (Fig. 7B). **Metasoma.** Petiole in lateral view with a very short peduncle, slightly longer than high, with a slightly concave anterior margin and a dorsum of node that more...
or less narrowly rounded, while posterior margin slightly convex (Fig. 7C); in dorsal view subcampanulate, longer than broad, with a relatively narrow anterior margin and slightly convex lateral margins. Subpetiolar process in lateral view acute toothed anterioventrally (Fig. 7C). Postpetiolar process in lateral view as long as high, anterior margin rising in a gentle slope towards the posterior margin and then abruptly descending (Fig. 7C); in dorsal view clearly larger than petiole, roughly pyriform, with a relatively narrow anterior margin and slightly convex lateral margins (Fig. 7B); postpetiolar sternite in lateral view slightly convex, with rounded anteroinferior corners (Fig. 7B). Gaster in lateral view elliptical (Fig. 7C). Sculpture. Mandibles longitudinally striate (Fig. 7A). Clypeus smooth and shining, antennal scape finely punctate. The posterior portion of the head longitudinally striate, with densely punctate spaces between them (Fig. 7A). Promesonotal rugae extend laterally, the lower part of mesopleuron and metapleuron longitudinally striate (Fig. 7C). Pronotum with finely transverse rugae, mesonotum densely transversely striate, and anterodorsal propodeum sparsely transversely striate, with shining declivity (Fig. 7B). Dorsum of petiole sparsely rugose and punctate (Fig. 7C). Gaster smooth and shining. Pilosity. Body entirely covered erect to suberect and yellowish hairs. Antennal scape with subdecumbent hairs. Coloration. Body reddish brown to blackish brown (Fig. 7).

Paratype workers. TL 5.99–6.34, HL 1.64–1.74, HW 1.37–1.48, CI 83.08–87.96, SL 1.31–1.46, SI 90.46–103.80, ED 0.32–0.35, PW 0.92–0.99, MSL 2.15–2.43, PL 0.61–0.71, PH 0.45–0.46, DPW 0.39–0.40, LPI 64.32–75.21, DPI 55.29–64.31 (n = 3).

Recognition. Manica shanyii sp. nov. can be easily distinguished from its congeners by the following characteristics: the entire dorsum of mesosoma exhibits transverse striation and punctae, and masticatory margin of mandibles only with seven teeth, comprising one large apical tooth, one secondary tooth, and followed by five smaller teeth. Distribution. Emei and Gongga Mountains in Sichuan, China.

Habitat. The nest of Manica shanyii sp. nov. was discovered in the Gongga Mountain National Nature Reserve and Emei Mountain National Nature Reserve, Sichuan, China. The sampled sites are positioned within a mixed coniferous broad-leaved forest, where the ants were found inhabiting dead wood on the forest floor covered with brown forest soil.

Etymology. This species is named after Professor Zhou Shanyi from Guangxi Normal University, China, in recognition of his significant contributions to the field of ant taxonomy in China.

*Manica yessensis* Azuma, 1955

Fig. 8


Type material. Unexamined, but high-resolution images of paratype worker (CASENT0900372, imaged by Ryan Perry) were reviewed.
Diagnosis. Head and gaster black, while other parts reddish brown. In lateral view, posterodorsal corner of propodeum obtusely angular. Petiole in lateral view longer than high, with a distinct dorsum, anterior margin of node concave and posterior slopes convex; subpetiolar process in lateral view acutely angled anteroventrally. Postpetiole

Figure 8. *Manica yessensis* worker (Paratype, images cited from https://www.antweb.org/, CASENT0900372, imaged by Ryan Perry) A head in full-face view B label C body in dorsal view D body in lateral view.
in lateral view higher than long; sternite of postpetiole anteroventrally produced as a blunt angle directed forward. Petiole and lateral face of postpetiole rugose-punctate.

**Recognition.** *M. yessensis* Azuma, 1955 is closely related to *M. bradleyi* (Wheeler, 1909), but it can be separated from the latter by the following characteristics: the posterodorsal corner of propodeum in lateral view is obtusely angular; the postpetiole in lateral view is higher than long; the sternite of postpetiole is anteroventrally produced as a blunt angle directed forward; and both the petiole and the lateral face of postpetiole exhibit rugose-punctate patterns.

**Distribution.** This species is found exclusively in the northern and central regions of Japan.

**Discussion**

Zharkov et al. (2023) described a Baltic amber – *Manica andrannae*, which from the Kaliningrad region of Russia (formerly part of the Palaearctic Region). This newly described taxon is the first fossil species of the genus *Manica*, serving as an important link in understanding the origin and evolution of this genus. Among the known nine species of the genus *Manica*, four extant species (*M. bradleyi, M. hunteri, M. invidia, M. parasitica*) and one extinct species (*†M. iviei*) are predominantly distributed in the western part of the Nearctic Region, two species (*†M. andrannae, M. rubida*) are concentrated in the western part of the Palaearctic Region, one species (*M. yessensis*) is found in Japan in the eastern part of the Palaearctic Region, and the newly discovered species (*M. shanyii*) is distributed in the southernmost part of the Palaearctic Region. Based on the current distribution, North America evidently serves as the center of species diversity for the genus *Manica* (Fig. 1). Zharkov et al. (2023) hypothesized that the genus *Manica* may have originated in the Nearctic Region and later dispersed to the Palearctic Region. However, based on the “Diversification rate hypothesis” (Wiens and Dykhuizen 2011), regions with high species diversity do not necessarily indicate older taxa in that area. Therefore, inferring the Nearctic Region as the center of origin for the genus *Manica* solely based on species distribution, although plausible, remains contentious. However, the discovery sites and formation times of fossils can provide valuable insights into the origin of species. Despite fossil distribution in both the Nearctic Region and the Palaearctic Region, fossil species of *†M. andrannae* in the Palaearctic Region was formed during the Middle to Late Eocene, while the *†M. iviei* in the Nearctic Region was formed during the Oligocene. Consequently, the fossil species in the Palaearctic Region are older, hinting that the earliest *Manica* might have been distributed in the Palaearctic Region, particularly in Europe, during the Eocene. Based on this, we hypothesize that *Manica* possibly originated in the mid-Eocene, with its center of origin in Europe within the Palaearctic Region, before dispersing to the Nearctic Region over long distances. As for species in East Asia, they might have originated from species in the Nearctic Region through the Bering Land Bridge or from European species dispersing to East Asia over long distances. Discovering new species or records of this genus in Central Asia
in the future could somewhat support the latter hypothesis. Of course, for a systematic elucidation of the origin and dispersal of *Manica*, future biogeographical studies based on phylogenetic relationships could be conducted.

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