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Discovery of the formerly Japan-endemic *Ponera kohmoku* Terayama, 1996 (Formicidae, Ponerinae) in Southeast China, and implications for understanding the ecology and biogeography of the species

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ABSTRACT. *Ponera kohmoku* is a species described in 1996 from Yaku-shima Island, and all known records to date have been limited to the southern portion of Japan. Here, new records of *P. kohmoku* are reported from Guangdong, Guangxi and Hong Kong in China, adding a fourth *Ponera* species to Hong Kong and Guangxi as well as the first nominal record of this genus to the Guangdong myrmecofauna. By integrating ecological information from past literature records of *P. kohmoku* with these new records from Southeast China, *P. kohmoku* is suggested to be a forest understory generalist in terms of habitat preference. The disjunct distribution of the species in southern Japan, Guangdong, Guangxi and Hong Kong raises the question about the biogeographic history of the species and the genus. Here, we propose and evaluate two hypotheses for such disjunct distribution: 1) the extinction of population from most parts of eastern mainland China, and 2) knowledge gap caused by the under sampling of cryptobiotic ants in mainland China.

Keywords	biogeography, ecology, distribution, biodiversity
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INTRODUCTION

The ant genus *Ponera* Latreille, 1804 contains 59 valid extant species (Pierce et al., 2019). Most *Ponera* species build nest in decaying logs or under rocks and forage mainly within the leaf litter and/or in soil (Taylor, 1967; Schmidt & Shattuck, 2014). A combination of small colony size (usually < 60 workers) and cryptobiotic lifestyle results in difficulties in sampling this ant genus (Wong & Guénard, 2017; Leong et al., 2019). Therefore, undersampling of *Ponera* has been noticed in many places, particularly in the Oriental realm where the species richness of *Ponera* peaks (Guénard & Dunn, 2012; Janicki et al., 2016; Guénard et al., 2017).

In the Chinese provinces of Guangdong, Guangxi and the Special Administrative Region of Hong Kong, which are located at the interface of the Oriental and Sino-Japanese realms, four *Ponera* species have been recorded: *P. sinensis* Wheeler, 1928, *P. guangxiensis* Zhou, 2001 and *P. paedericera* Zhou, 2001 are recorded from Guangxi, and *P. sinensis*, *P. guangxiensis* and *P. tudigong* Pierce, Leong, and Guénard, 2019 from Hong Kong, while no nominal species had been recorded from Guangdong prior to this study. The only record of *P. sinensis* from Hong Kong is the type specimen, and with no additional specimens collected to date (Wheeler, 1928; Pierce et al., 2019). Extensive ant surveys carried out in the past decade have yielded the other two species to Hong Kong, *P. guangxiensis* and *P. tudigong,* mainly through the use of pitfall traps and Winkler extractor sampling (Pierce et al., 2019).

Here we present a new species record of the formerly Japan-endemic *Ponera kohmoku* Terayama, 1996 in Guangdong, Guangxi and Hong Kong. By combining the information of previous records of *P. kohmoku* from Japan and that of our new records from Southeast China, we discuss the ecology and biogeography of this species.

MATERIALS AND METHODS

Collection methods

Workers of *P. kohmoku* from Hong Kong were discovered during log dissection on 19th February 2021 and 2nd October 2023. Fourteen workers in total were hand-collected at the site using a pair of soft forceps. Specimens from Guangdong and Guangxi were collected by J.R. Fellowes in the late 1990s and deposited at the Hong Kong Biodiversity Museum, which were revisited and identified during this study.

Specimen comparison

To compare the morphology of the specimens from Hong Kong, Guangdong and Guangxi with those from Japan, two *P. kohmoku* workers were borrowed from Prof. Seiki Yamane (Kagoshima, Japan).

Morphology

The morphological traits measured and their respective terminologies are detailed below and follow those used in Leong and collaborators (2019). Measurements are reported in millimetres to three decimal places.

HL Head length. The maximum length of the head, measured as a straight line between the centre of the posterior cephalic margin and the centre of the anterior clypeal margin. Measured in full-face view.

HW Head width. The maximum width of the head, measured as the longest straight line from one lateral margin to the other. Measured in full-face view.

ML Mandible length. The maximum length of the mandible, measured as a straight line from the mandibular insertion to the tip of the apical tooth, with the mandible in dorsal view.

WL Weber's length. The maximum length of mesosoma in profile view, measured from the inflection of the pronotum to the posterior propodeum.

PeH Petiole height. The maximum height of the petiole, measured as the longest straight line from the ventral margin of the fenestra to the dorsal margin of the petiole. Measured in profile view.

PeNL Petiolar node length. The length of the node of the petiole, measured as a straight line from the anterior margin of the petiole immediately above the dorsal base of the anterior petiolar tubercle to the posterior margin of the petiole. Measured in profile view.

PeW Petiole width. The maximum width of the petiole, measured as the longest straight line from one lateral margin of the petiole to the other. Measured in dorsal view.

PrW Pronotal width. The maximum width of the pronotum, measured as the longest straight line from one lateral margin of the pronotum to the other, measured in dorsal view.

SL Scape length. The maximum length of the scape, measured as a straight line from the base of the scape (excluding the basal neck and condyle). Measured in full-face view.

ATL Abdominal tergum III length. The maximum length of the 3rd abdominal tergum, which is the 1st gastral tergum. This is measured from the centre of the anterior margin to the centre of the posterior margin. Measured in dorsal view.

ATW Abdominal tergum III width. The maximum width of the 3rd abdominal tergum, which is the 1st gastral tergum. This is measured as the longest straight line from one lateral margin to the other. Measured in dorsal view.

ATI Abdominal tergum III (= 1st gastral tergum) index. ATL/ATW × 100.

CI Cephalic index. Calculated as HW/HL × 100.

DPeI Dorsal petiole index. Calculated as PeW/PeNL × 100.

LPeI Lateral petiole index. Calculated as PeNL/PeH × 100.

PeI Petiole index. Calculated as PeW/PrW ×100.

SI Scape index. Calculated as SL/HW × 100.

Imaging and measurements

Stacked images of specimens were taken using a Leica DFC450 digital camera mounted on a Leica M205C stereomicroscopes (Wetzlar, Germany). The images were processed and the morphological traits were measured using Leica Application Suite V4 software with specimens positioned specifically for each measure.

RESULTS

Specimen collection

In Hong Kong, *Ponera kohmoku* was found within three heavily decayed logs and a 40 cm tall standing dead trunk on the forest floor of a subtropical evergreen secondary forest. The canopy was composed of a mixture of tree species, including *Litsea acutivena* Hayata, 1915, *Lithocarpus haipinii* Chun, 1947, *Acer tutcheri* Duthie, 1908, *Cornus hongkongensis* (Hemsl.) Hutch. and *Anneslea fragrans* Wall., whereas the understorey consisted of small trees, shrubs and vines such as *Rhododendron simsii* Planch., *Fissistigma glaucescens* (Hance) Merr. and *Lirianthe championii* (Benth.) NH Xia & CY Wu (Fig. 1). On 19th February 2021, five workers were hand-collected within the nest tunnels, while an undetermined number of other nestmates were left on site. An attempt to collect a colony was made on 2nd October 2023, but only seven workers from a colony fragment were collected from a decaying log and two separate workers were collected from another decaying log and a standing dead trunk respectively.

In Guangxi, one worker was collected in a broadleaf forest /shrubland open habitat (J. Fellowes Pers. Comm.). No information is known about the worker collected in Guangdong.

Materials examined:
***Ponera kohmoku* Terayama, 1996** (Fig. 2 - 5)

HKBM: Hong Kong Biodiversity Museum, the University of Hong Kong, Hong Kong

Hong Kong: Five workers, 22.4137°N 114.2442°E, 565 m alt., Hong Kong, Tiu Shau Ngam, 19 II 2021, TKC Leung leg (TKCL042, TKCL043, TKCL044, TKCL045, TKCL046), deposited at the HKBM. Nine workers (one worker from MTH527 was dry mounted and measured, while the other eight workers were stored in 70% ethanol), 22.41266°N 114.24046°E, 451 m alt., Hong Kong, Tiu Shau Ngam, 02 X 2023, MT Hamer leg. (MTH527 (ANTWEB1010227), MTH531 & MTH534).

Guangdong: One worker, Qimuzhang, Wuhua County, 5 IV 1997, J. Fellowes leg (MBS006531), deposited at the HKBM.

Guangxi: One worker, 1260 m alt., Da Yao Shan, Leye County, Baise, China, 16 IX 1998, J. Fellowes leg, (MBS006532), deposited at the HKBM.

Japan: One worker, Japan, Kyushu, Ohsumi Peninsula, Minamiōsumi-cho, near Hetsuka, 23 VII 2020, Sk. Yamane leg (JP20-SKY-061), deposited at Seiki Yamane's laboratory. One worker, 33.6418°N 130.5299°E, 120m alt., Japan, Fukuoka Pref, Hisayama-machi, Kutara, 28 IX 2020, YN Minoshima #12, deposited Prof. Seiki Yamane's collection.

Measurements (mm) and indices:
Workers from Hong Kong (n = 6): HL 0.856–0.900; HW 0.699–0.756; SL 0.625–0.663; A06L 0.053–0.066; A07L 0.064–0.072; A08L 0.080–0.093; A09L 0.100–0.116; A10L 0.104–0.130; PrW 0.569–0.628; WL 1.182–1.343; PeH 0.650–0.673; PeNL 0.308–0.366; PeW 0.426–0.498; ATL 0.629–0.704; ATW 0.707–0.744; CI 81.0–84; SI 87.1–92.0; PeI 67.8–79.9; LPeI 45.8–55.5; DPeI 122–156; ATI 89.0–95.1.

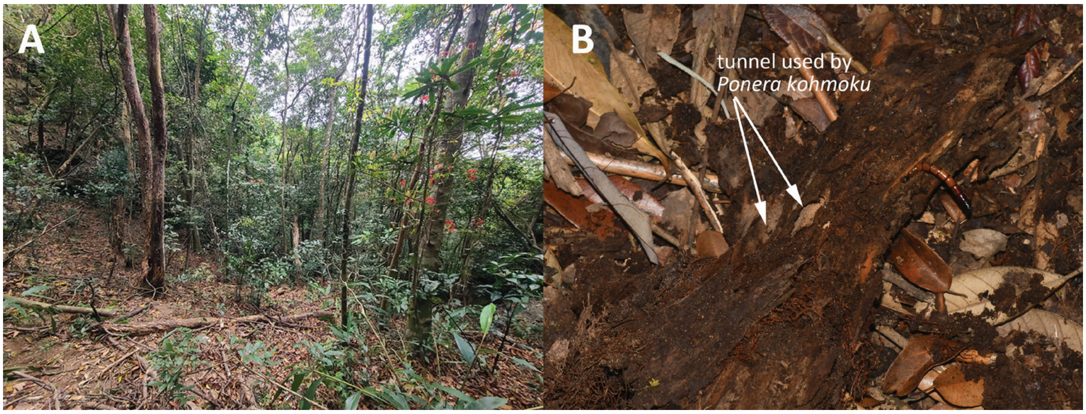

Fig. 1. Photos of the **(A)** secondary forest hill slope habitat and **(B)** one of the heavily decayed logs where the *Ponera kohmoku* from Hong Kong were found.

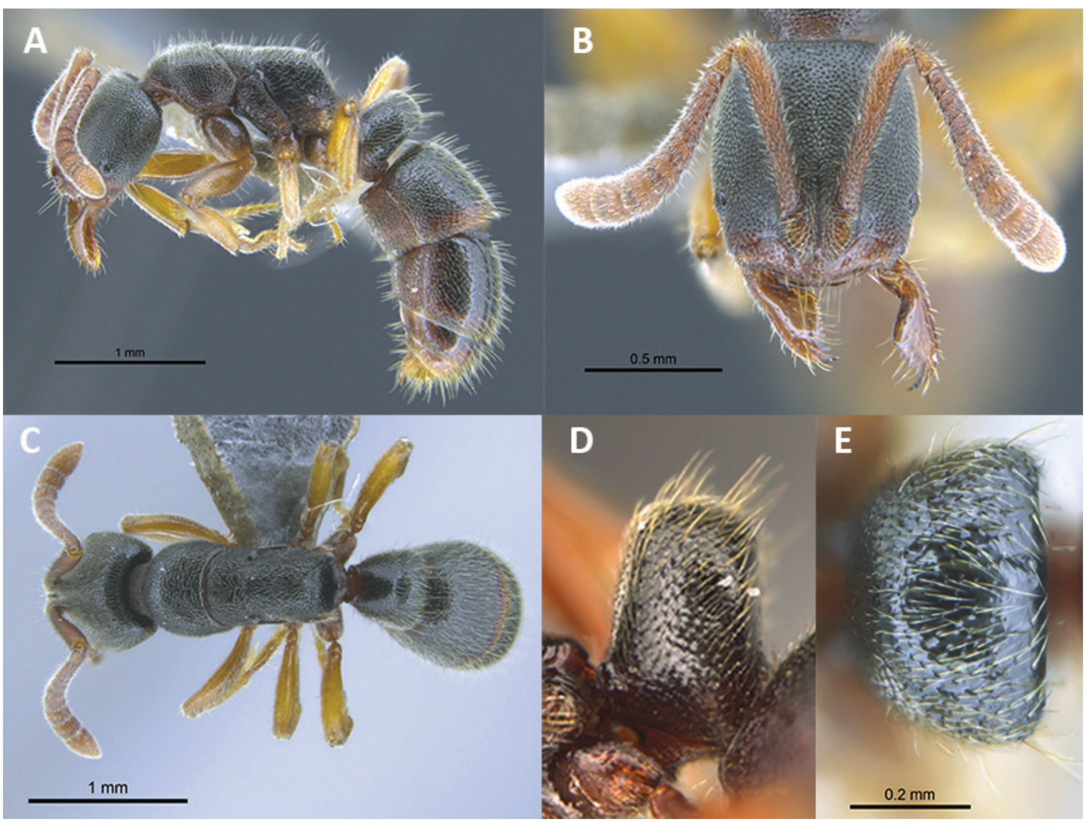

Fig. 2. (A) Habitus, (B) full face view, (C) dorsal view, (D) lateral view of petiolar node, and (E) dorsal view of petiolar node of *Ponera kohmoku* (Accession code TKCL046) from Hong Kong.

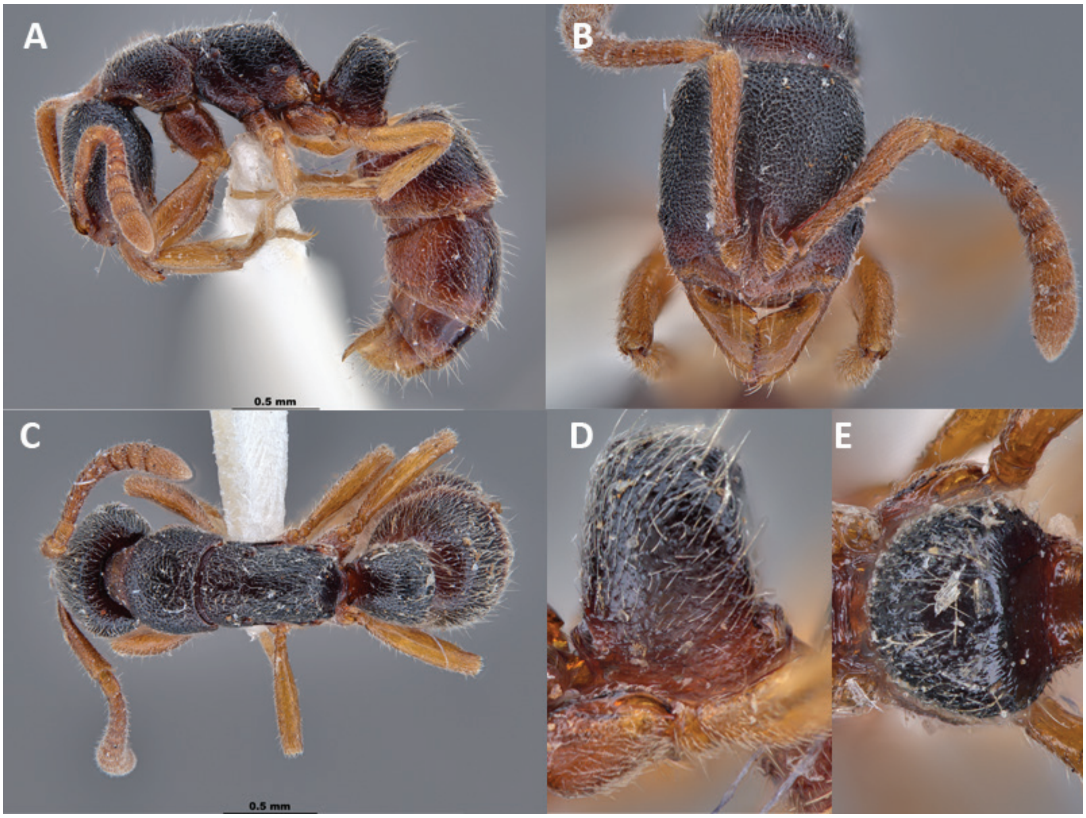

Fig. 3. (A) Habitus, (B) full face view, (C) dorsal view, (D) lateral view of petiolar node, and (E) dorsal view of petiolar node of *Ponera kohmoku* (Accession code MBS006531) from Guangdong.

Worker from Guangdong (n = 1): HL 0.824; HW 0.708; SL 0.657; A06L 0.061; A07L 0.068; A08L 0.09; A09L 0.110; A10L 0.123; PrW 0.576; WL 1.236; PeH 0.648; PeNL 0.360; PeW 0.444; ATL 0.681; ATW 0.734; CI 85.9; SI 92.8; PeI 77.1; LPeI 55.6; DPeI 123; ATI 92.8.

Worker from Guangxi (n = 1): HL 0.832; HW 0.668; SL 0.618; A06L 0.051; A07L 0.057; A08L 0.078; A09L 0.089; A10L 0.111; PrW 0.563; WL 1.168; PeH 0.622; PeNL 0.357; PeW 0.430; ATL 0.644; ATW 0.722; CI 80.3; SI 92.5; PeI 76.4; LPeI 57.4; DPeI 120; ATI 89.2.

Species identification: Based on the diagnosis of *Ponera kohmoku* and the East Asian *Ponera* key (Leong et al., 2019), this species can be distinguished by a combination of the following features: large compound eyes with over 20 ommatidia, long antennal scape, distinct metanotal groove, and petiolar node shape. We also compared the specimens from South East China with those from Japan (the type locality), as well as with morphological measurements to further confirm the identity of the specimens collected in Hong Kong as *P. kohmoku*. All the measurements of the specimens collected in Guangdong, Guangxi and Hong Kong fall within the range or overlap with the values provided in Terayama (1996) for 10 measurements collected from 11 type specimens. Only the value of the scape index is slightly lower in our specimens in Hong Kong (SI= 87.1–90.3) than on the type specimens (SI= 91–97). Nonetheless, the scape index of the specimens from Hong Kong overlaps with the measurement from Leong and collaborators (2019) (SI= 82–91).

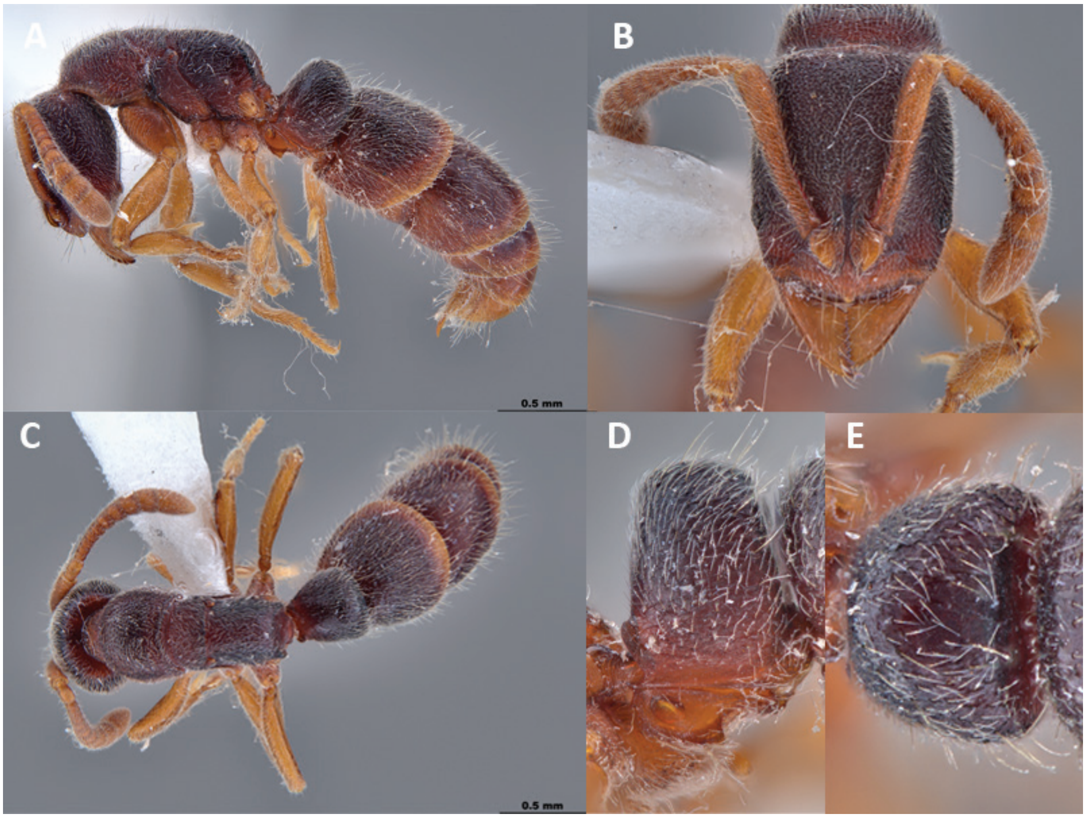

Fig. 4. (A) Habitus, (B) full face view, (C) dorsal view, (D) lateral view of petiolar node, and (E) dorsal view of petiolar node of *Ponera kohmoku* (Accession code MBS006532) from Guangxi.

DISCUSSION

All of the 14 specimens collected from Hong Kong and the two specimens from Guangdong and Guangxi match the morphology of *Ponera kohmoku* collected from Japan, as well as the description in Terayama (1996) and Leong et al., (2019). We hereby confirm the presence of *P. kohmoku* in Guangdong, Guangxi and Hong Kong.

Ecology of *Ponera kohmoku*

The specimens from Hong Kong were collected from hill slopes covered by subtropical evergreen secondary forest at 451-565 m elevation. The overall habitat was similar to the secondary evergreen forest described in Harada et al., (2011) from a Japanese sampling location. The specimen from Guangxi appears to have been collected in some kind of forested habitat, although the exact definition is unclear, and at an elevation of 1260 m. In Japan, *P. kohmoku* was found in numerous habitats, including lowland bamboo forest as low as 100 m in elevation (Fukumoto, et al., 2013), costal secondary forest grown on lava plane (Harada et al., 2008) and primary (Hosoishi et al., 2007) or secondary laurel forest as high as 700 m (Matsumura & Yamane, 2012; Harada et al., 2013). Amongst secondary laurel forest where *P. kohmoku* was found, the dominant vegetation species differed, implying *P. kohmoku*'s ability to inhabit lowland subtropical forest in general (Harada et al., 2011). The wide variety of shaded habitats inhabited by *P. kohmoku* suggest that in terms of habitat preference, the species is a forest floor generalist.

When disturbed during the process of log dissection, the *P. kohmoku* workers, like other *Ponera* species (e.g. *P. sinensis, P. guangxiensis*), did not show any attempts to defend or attack, but rather hid immediately into the unexposed section of the nest tunnels. While the colony size of *P. kohmoku* in Hong Kong was not estimated, with only a few workers collected, this species is known to have small colony size of about 35 individuals (Terayama et al., 2014).

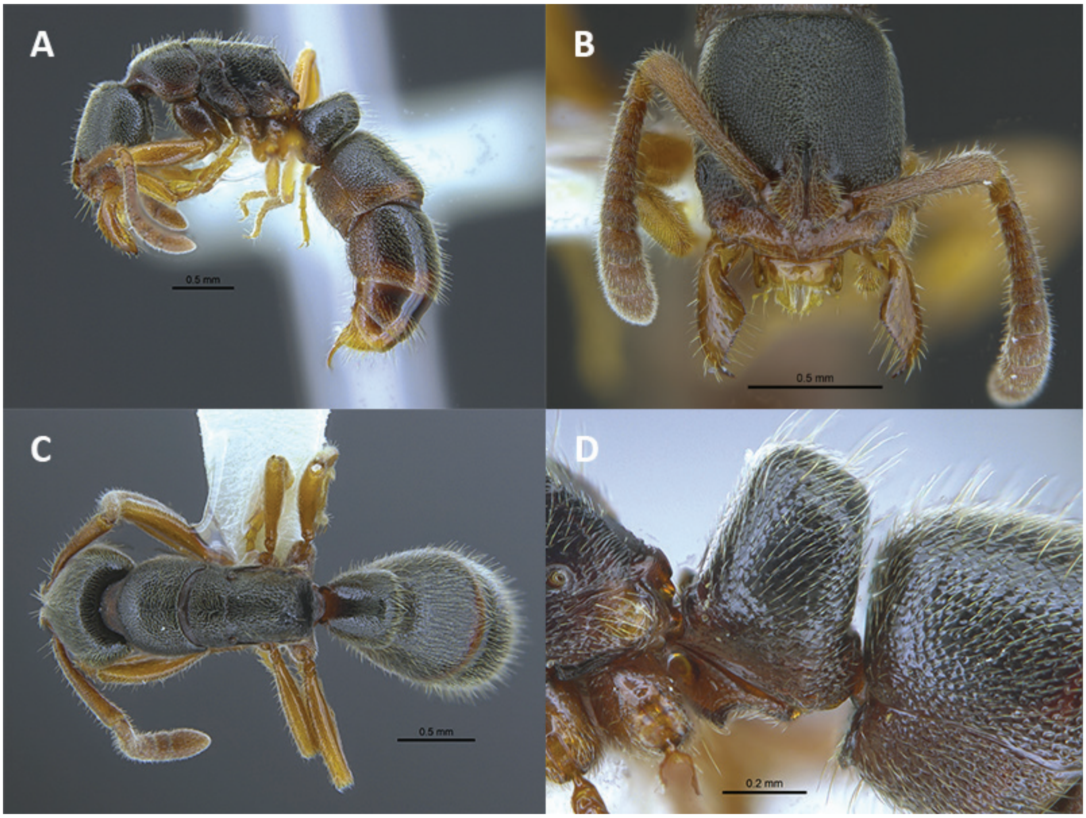

Fig. 5. (A) Habitus, (B) full face view, (C) dorsal view and (D) lateral view of petiolar node of *Ponera kohmoku* from Ohsumi Peninsula, Kagoshima Prefecture, Japan.

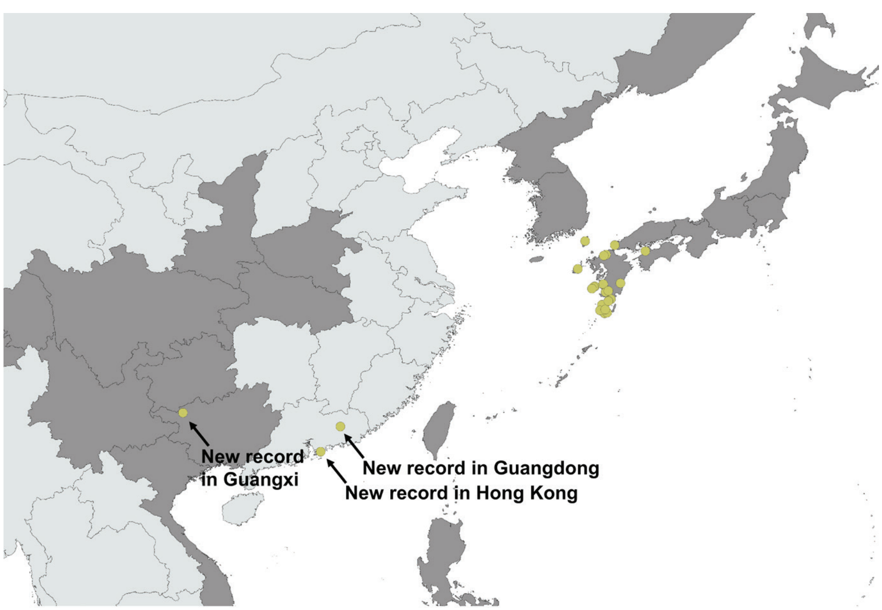

Fig. 6. Distribution of *Ponera kohmoku* in East Asia. Yellow dots show the known distribution of *P. kohmoku* in South Japan, Guangdong, Guangxi and Hong Kong. The background map shows the current knowledge of the genus *Ponera* in East Asia with regions with known records of *Ponera* species shown in dark grey, and regions without nominal species records in light grey.

Biogeography of *Ponera kohmoku*

The discovery of *Ponera kohmoku* from Guangdong, Guangxi and Hong Kong not only adds a new *Ponera* species to the ant diversity of these regions and mainland Asia, but also raises questions about the biogeography of *P. kohmoku*. The known distribution of *P. kohmoku* so far was limited to southeastern Japan including the Koshiki Islands, Kyushu, the Osumi Islands, Shikoku, and Tsushima island (Yamane et al., 1999; Yamane & Fukumoto, 2017; Guénard et al., 2017) and is, thus far, unknown from the central and southern Ryukyu Islands or Taiwan. Given the long distance (> 1800 km, Fig. 6) between the new localities in Southeast China and the southernmost record in Japan, such discontinuous distribution was unachievable by a single flight dispersal event. To explain this disjunct distribution, the following hypotheses are discussed: 1) past extinction of more widespread population in mainland China, and 2) undersampling of cryptobiotic ants from mainland China.

One of the explanations for the disjunct distribution of *P. kohmoku* may lie in the extinction of the species in mainland China and/or Taiwan. Eastern China, Taiwan and western Japan were continuously connected by land bridges from 10 to 1.7 million years ago (Kitamura & Kimoto, 2004), as well as intermittently connected during the last glacial maxima in mid-Pleistocene (Kawamura, 1998). Land bridges, including the land bridge that connected Japan and mainland China via the Korean Peninsula, made dispersal across mainland China, Taiwan and Japan possible, thus allowing for the faunal and floral exchanges over both a long-term geological time scale and short-term climatic scale (Kawamura, 1998), with important consequences on the distribution of the current East Asian ant fauna (Wepfer et al., 2016). This is also reflected in the *Ponera* genus by the fact that all native species recorded in Japan, except for *P. kohmoku* until now, were also found either in mainland China (*P. scabra* Wheeler, 1928) and Taiwan (*P. alisana* Terayama, 1986, *P. bishamon* Terayama, 1996, *P. japonica* Wheeler, 1906, *P. takaminei* Terayama, 1996 and *P. tamon* Terayama, 1996) (Yoshimura et al., 2009; Leong et al., 2019). Similarly, it is possible for *P. kohmoku* to have spread amongst mainland China, Taiwan, Hong Kong and Japan through these land bridges. Subsequent habitat and climate change in East China and Korean Peninsula during the glacial–interglacial oscillations in Quaternary period have caused local extinction of various fauna and floral and perhaps *P. kohmoku* in the area, resulting in today's disjunct distribution (Sandel et al., 2011; Huang et al., 2023). A phylogenetic study of the species would be needed to date the time of, if any, the vicariant event.

Alternatively, the apparent disjunct distribution of *P. kohmoku* could result from sampling biases of cryptobiotic ants within mainland China. Since methods for sampling subterranean or leaf litter-dwelling ants such as Winkler extraction and subterranean traps have been rarely used by ant researchers from mainland China, *Ponera* from mainland China is undoubtedly understudied (Guénard & Dunn, 2012; Wong & Guénard, 2017). In addition, because *Ponera* can be perceived as a taxonomically challenging genus (Leong et al., 2019, Pierce et al., 2019), this may have prevented the identification of individuals collected in the region such as those presented here from Guangdong and Guangxi provinces collected one year and two years respectively after the species description which remained unidentified for over 25 years. This is also reflected by the absence of published records of nominal *Ponera* species from the entire eastern maritime façade of the Chinese provinces spanning from Hainan to Liaoning (Guénard & Dunn, 2012; Janicki et al., 2016; Guénard et al., 2017), as well as for some other inland provinces (e.g. Anhui, Hunan, Jiangxi, Fig. 6). Indeed, to this point, only eight of the 23 Chinese provinces, all on the central or western part of China, have records of *Ponera*. While this could reflect a biogeographic pattern, recent sampling and taxonomic efforts in Hong Kong where four species are now recorded over this small territory highlight the lack of sampling in the region, as in other widespread and abundant leaf-litter ant genera (e.g. *Strumigenys* Smith, 1860 – Tang et al., 2019, Brassard et al., 2020, *Stigmatomma* – Hamer et al. 2023, *Nylanderia* Emery, 1906 – Silva et al. 2023). It would thus seem very likely that in provinces such as Fujian or Zhejiang which retain important natural areas, including primary forests (e.g. Huboliao Nature Reserve and Xitianmu Natural Reserve), and large topographic variations, that the apparent absence of

Ponera species simply results from under sampling within the area. Therefore, further sampling effort should be conducted to sample cryptobiotic ants in Eastern and Southeast China to verify the actual distribution range of *P. kohmoku* and its congeneric species in the area.

In contrast to the undersampling observed in mainland China, ant sampling and taxonomic efforts in the Ryukyu islands in Japan as well as in Taiwan have been more extensive (Yamane et al., 1999; Terayama, 2009; Yamane & Fukumoto, 2017). The apparent absence of *P. kohmoku* from the Ryukyu islands south of Yakushima and Taiwan may suggest that the species have been unable to cross the sea barrier south of Yakushima Island and has reached mainland China through the Korean Peninsula land bridge. The direction of movement is, however, unknown given that the origin of the species is uncertain, and thus the movement can possibly be the other way round. The central and southern Ryukyu islands have always if not mostly been separated from Yakushima and Kyushu by sea barrier at least since the mid-Pleistocene (Kawamura et al., 2016), thus imposing difficulties for *P. kohmoku* to colonize these islands.

A third hypothesis can be proposed though, which does not rely on a natural distribution of *P. kohmoku* but on its introduction due to human activity. Indeed, Hong Kong is a major hub for the global trade which has led to many introductions within the region, including for ground-dwelling and leaf-litter ants (Guénard 2018; Tang et al., 2019; Hamer et al. 2023, Silva et al. 2023; unpublished records). This hypothesis seems, however, unlikely due to the habitat and locality where *P. kohmoku* was collected. Here the specimens from Hong Kong were collected in a natural forested habitat, although not pristine, and located at 400 m horizontally from the nearest settlement. This would thus be in sharp contrast with other exotic and tramp species encountered in Hong Kong, often found within anthropogenic habitat characterized by high and frequent disturbance levels (e.g. Guénard 2018; Tang et al., 2019, Hamer et al. 2023). As for the Guangdong and Guangxi specimens, both Qimuzhang and Dayaoshan are situated within protected area and are composed of either secondary or primary forests (Luo & Zheng, 2002; Deng et al., 2004). This hypothesis thus appears as the least likely, even though it should be noted that some exotic species possess the ability to colonize and spread within more natural habitats (Hoffmann & Parr 2008), including in Ponerinae (Guénard & Dunn 2010).

While two hypotheses have been explored, the most plausible hypothesis appears to be the second one stating a more widespread but unrecorded distribution of this species in other regions due to limited sampling and taxonomic efforts in the region. This is also the most significant as it is not only limited to *P. kohmoku*, nor the *Ponera* genus, but to potentially hundreds of ant species and dozens of genera that remain poorly studied in the region, ultimately providing us a partial and bias perception of ant distribution in East Asia.

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