Syscia chinensis sp. nov., a tiny novel ant species of *Syscia* (Hymenoptera, Formicidae, Dorylinae) from Southwest China

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ABSTRACT. The ants of genus *Syscia*, are cryptic with an unequal distribution in Asia and the Americas; Currently, there are 34 species known in the New World, but only a mere 10 species are recognized in Asia. The New World species have been systematized, whereas Old World species are currently still at the stage of isolated species descriptions. Herewith a new species, namely *Syscia chinensis* **sp. nov.**, is described and illustrated based on the worker caste. *S. chinensis* is the first species reported with 10-segmented antennae in this genus, and it is also one of the smallest minority species in this genus. These two characteristics readily distinguish the new species, and these morphological differences are supported by a phylogenetic analysis. A key based on the worker caste is provided for the known Asian species.

Keywords	Dorylinae, 10-segmented antennae, Yunnan province, China, taxonomy, Phylogenetic
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INTRODUCTION

The ant genus *Syscia*, initially defined by Roger in 1861 with the Sri Lankan species *S. typhla* as the type species, now comprises 42 valid species (Aswaj et al. 2021; Bolton 2024). These species are recorded in Asia, North America, and South America, exhibiting a pattern of disjunct distribution (Borowiec 2016) in 16 countries or regions (Borowiec 2016; Jaitrong et al. 2020; Aswaj et al. 2021; Longino and Branstetter 2021; Bolton 2024). These ants are often found in soil or leaf litter and are considered part of the cryptobiotic fauna (Jaitrong et al. 2020; Longino & Branstetter 2021).

In more than 160 years since the establishment of the genus Syscia, the taxonomic status of the genus has undergone many changes. Because of its similarity to the genus Cerapachys Smith, 1857, myrmecologists have different views in the process of taxonomic research. Dalla Torre (1893), Forel (1900) and Bingham (1903) regarded Syscia as a valid genus, while Wheeler (1902, 1910, 1922), Emery (1902, 1911), Forel (1917) and Donisthorpe (1943) regarded it as a subgenus of Cerapachys. Kempf (1972) and Brown (1975) treated Syscia as a junior synonym of Cerapachys. It was not until the past decade that myrmecologists reconfirmed the taxonomic status of Syscia as a valid genus through phylogenetic inference from molecular data (Brady 2014; Borowiec 2016).

Borowiec (2016) defined the diagnostic features of *Syscia* as: Antennae with nine or 11 segments; eyes small or absent; body with densely sculptured and abundant pilosity; body color relatively uniform, with yellow, red or dark brown but never black; posterior tarsus basal segment widened distally, with a light-colored patch of cuticle medially (flexor); abdominal tergite iv anteriorly folding over sternite.

Yamane & Mizuno (2024) described two species of Syscia from Sabah, Borneo. Currently, there are 34 species known in the New World, with ten species recognized in Asia (Bolton 2024). Here we report on a new species with 10-segmented antennae from China. Before this study, three Syscia species had already been recorded in China. Du et al. (2024) removed S. typhla Roger 1861 from the ant fauna of China, moved Ooceraea guizhouensis (Zhou 2006) into Syscia, and added two new species: S. arcodorsa Du et al., 2024 and S. zhoui Du et al., 2024. Including the new species described herein, there are four species known from China. A key to all known Asia species and a map of the distribution data of the Chinese species is provided.

MATERIALS AND METHODS

The specimens were collected in the field by sample-plot and search-collecting methods (e.g., Xu 2002) in Huanglianshan National Nature Reserve, Lvchun County, Honghe Prefecture, Yunnan Province, China, between 102. 03930 ~ 102. 61638E, 22. 50525 ~ 22. 92658N (Fig. 1). Thirteen workers were collected from the same soil nest. All the samples were preserved in 75% ethanol for transport back to the insect herbarium of the Kunming Natural History Museum of Zoology. The specimens were cleaned and organized in the laboratory. Subsequently, they were prepared as dry specimens and pointmounted. The specimens were identified using a SDPTOP-SZM stereomicroscope, photographs were taken of the multilayered superimpositions using a Keyence VHX-6000 digital microscope, and the images were combined into graphics using Adobe Photoshop 2020. Maps were constructed using the software package ArcGIS v. 10.8.2. Comparisons were made with species from China (Zhou 2006; Du et al. 2024). Morphological terminology follows Borowiec (2016), Jaitrong et al. (2020) and Aswaj et al. (2021). The key was prepared using the examined specimens, images available on AntWeb (2024) and AntWiki (2024), and original descriptions of the species. All measurements are in millimeters.

- TL Total length: total length of head, mesosoma, petiole and gaster in lateral view
- HL Head length: length from the anterior of clypeus to the posterior of head in full-face view
- HW Head width: width of head in full-face view
- SL Scape length: straight-line length of the antennal scape, excluding the basal constriction or neck
- PrW Pronotal width: width of pronotum in dorsal view
- WL Weber's length: diagonal length of mesosoma in lateral view
- PL Petiolar length: length of petiole in lateral view (excluding helcium)
- PH Petiolar height: height of petiole in lateral view (including subpetiolar process)
- PW Petiolar width: width of petiole in dorsal view
- PpL Postpetiolar length: length of postpetiole in lateral view (excluding helcium)
- PpH Postpetiolar height: height of postpetiole in lateral view
- PpW Postpetiolar width: width of postpetiole in dorsal view

- AIVL abdominal tergite IV length: length of abdominal tergite IV in lateral view
- AIVH abdominal tergite IV height: height of abdominal tergite IV in lateral view
- AIVW abdominal tergite IV width: width of abdominal tergite IV in dorsal view
- CI Cephalic index: $HW/HL \times 100$
- SI Scape index: $SL/HW \times 100$
- PI1 Petiolar index one: $PL/PH \times 100$
- PI2 Petiolar index two: $PW/PL \times 100$
- PPI1 Postpetiolar index one: $PPL/PPH \times 100$
- PPI2 Postpetiolar index two: PPW/PPL × 100
- AIVI1 abdominal tergite index one: AIVL/AIVH $\times 100$
- AIVI2 abdominal tergite index two: AIVW/AIVL × 100
- WI Waist index: PPW/PW × 100

To confirm the taxonomic status of Syscia chinensis sp. nov. and evaluate its phylogenetic placement within the genus, we generated mitochondrial COI sequences for comparative analysis with published data from other Syscia species. DNA extraction of tissue fragments from ants was performed using the TSINGKE TSP202-50 Trelief® Hi-Pure Animal Genomic DNA Kit following manufacturer instructions. The standard cytochrome oxidase subunit I (COI) barcoding fragment (Hebert et al. 2003) was amplified using the primers LCO1490 (GGTCAA-CAAATCATAAAGATATTGG) and HCO2198 (TAAACTTCAGGGTGACCAAAAAATCA) (Folmer et al. 1994). Amplification was performed using TSINGKE Gold Mastermix (green), PCR reactions contained. PCR was performed using an initial denaturation step of two min at 98 °C, followed by 30 cycles of 10 s at 98 °C, 10 s at 50 °C and 10 s at 72 °C, and finishing with an extension of five min at 72 °C. The amplified PCR products were subjected to agarose gel electrophoresis (two ul sample + six ul bromophenol blue) at 300V for 12 min to obtain the identification gel graphs. The products were purified and sequenced by Tsingke Biotechnology (Beijing) Co., Ltd., using the same primers as in PCR. Sequences were edited using SeqMan in Lasergene 7.1 (DNASTAR Inc., Madison, WI, USA) and MEGA 11 (Tamura et al. 2021).

The COI sequences were compared to 35 COI sequences of subfamily Dorylinae species (33 *Syscia* and two outgroup specimens from the genus *Ooceraea* Roger, 1862 and *Chrysapace* Crawley, 1924) downloaded from the National Center for Biotechnology Information (NCBI) GenBank database using PhyloSuite v1.2.2 (Zhang 2020), for which data were extracted from Borowiec (2019), Branstetter et al. (2017), Longino & Branstetter (2021) and Yamada & Eguchi (2019), with their accession numbers listed in Suppl Table S3.

Sequences were aligned using ClustalW (Thompson et al. 2002) in MEGA 11 (Tamura et al. 2021) with default parameters. Genetic divergence (uncorrected p-distance) between species was calculated in MEGA 11. The best substitution model HKY+G+I was selected using the Akaike Information Criterion (AIC) in ModelFinder (Nei and Kumar 2000). The evolutionary history was inferred by using the Maximum Likelihood method based on the Hasegawa-Kishino-Yano model, and nodal support was estimated by 1,000 rapid bootstrap replicates in MEGA 11. Bayesian Inference phylogenies were inferred using MrBayes v3.2.7a (Ronquist et al., 2012) under GTR+I+G+F model (2 parallel runs, 2000000 generations, average standard deviation of split frequencies: 0.008), in which the initial 25% of sampled data were discarded as burn-in. Phylogenetic trees were edited with iTOL v5 (Letunic and Bork 2021).

Institutional abbreviations

KIZ Kunming Natural History Museum of Zoology, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, Yunnan Province, China

SWFU Insect Collection, Southwest Forestry University, Kunming, Yunnan Province, China

GXNU Insect Collection, Guangxi Normal University, Guilin, Guangxi, China



Fig. 1. The sampled sites of four species of genus *Syscia* distributed in China (Source: Drawing approval number: GS (2019) 1823. ArcGIS v. 10.8.2.) and habitat at the type locality of *S. chinensis* **sp. nov.** (This map image can be reproduced).

TAXONOMIC RESULTS

Syscia chinensis sp. nov. Chen, 2025 https://zoobank.org/DA141DA3-6EEC-4EA9-A592-2DA513DD416E Figs. 2 (A-D)

Etymology: The name refers to the terra typica China.

Type material. *Holotype:* worker, CHINA: Yunnan Province, Honghe Hani and Yi Autonomous Prefecture, Lvchun County, Banpo Township, Mohelongtang, 22.61721 N, 102.33585 E (Fig. 1), 1263 m above sea level, from soil in mixed coniferous and broad-leaved forest, 13.iv.2023, leg. Chao Chen, No. KIZ20230160 (KIZ). *Paratypes*: five workers, same data as holotype. KIZ20230160A and KIZ20230160B (SWFU); KIZ20230160C and KIZ20230160D (GXNU); KIZ20230160E (KIZ) **Description. Holotype worker:** TL 2.52 HL 0.53 HW 0.43 SL 0.21 PrW 0.31 WL 0.68 PL 0.26 PH 0.36 PW 0.26 PpL 0.31 PpH 0.37 PpW 0.38 AIVL 0.48 AIVH 0.39 AIVW 0.47 CI 81 SI 49 PI1 72 PI2 100 PPI1 73 PPI2 123 AIVI1 123 AIVI2 98 WI 146. **Paratype workers:** (n = 5) (Supp 2. Table S1): TL 2.40-2.69 HL 0.49-0.54 HW 0.41-0.43 SL 0.21-0.25 PrW 0.27-0.31 WL 0.62-0.67 PL 0.22-0.25 PH 0.31-0.36 PW 0.26 PpL 0.30-0.37 PpH 0.38-0.39 PpW 0.37-0.39 AIVL 0.48-0.61 AIVH 0.37-0.42 AIVW 0.47-0.50 CI 78-84 SI 51-59 PI1 61-79 PI2 102-120 PPI1 81-96 PPI2 99-130 AIVI1 124-146 AIVI2 78-103 WI 142-151.

In full-face view (Fig. 2A): Head rectangular, longer than broad, lateral margin moderately convex, posterior margin straight and posterior corners narrowly rounded. Frontal carinae extend posteriorly to less than ¹/₃ head length. Clypeus short, anterior margin weakly convex. Mandibles triangular, masticatory margin denticulate. Eyes absent. Antennae 10-segmented, scape short,



Fig. 2. *Syscia chinensis* **sp. nov.** worker (Holotype, imaged by Chao Chen) (A) head in full-face view (B) Petiolar node in lateral view (C) body in lateral view (D) body in dorsal view.

widened distally, not reaching mid-length of head, antennal segment (x) significantly larger than the rest of the antennal segments (ii-ix).

In lateral view (Fig. 2B, C): Mesosoma in profile view with slightly straight dorsal outline, lateral face of pro-mesonotum suture only reaches half the height of the side of mesosoma, unfused up to notal surface. Mesometapleural groove weakly impressed, transverse groove absent. Pleural endophragmal pit concavity present. Propodeal declivity moderately concave, with a distinct thin rim. Propodeal lobes present, well developed. Petiolar node (excluding sternite) square, roughly equal in length and height; dorsal outline weakly convex; anterior and posterior margins slightly straight. Subpetiolar process subtriangular, with ventral outline concave. Ventrolateral surface of petiole above the subpetiolar process with carinae. Postpetiole slightly higher than long, dorsal outline slightly convex; postpetiolar sternite shallow, ventral margin moderately convex, anteroventrally produced into a blunt angle.

In dorsal view (Fig. 2D): Mesosoma elongate with almost parallel lateral sides, anterior margin convex, cervical shield present, posterior margin weakly concave. Promesonotal suture and metanotal groove absent. Petiole subrectangular, slightly broader than long, lateral margins slightly convex, anterior and posterior margins slightly straight. Postpetiole larger than petiole, trapezoidal, anterior margin straight, posterior margin slightly concave, posterior margin longer than anterior margin, lateral margins slightly convex. Abdominal tergite iv (second gastral tergite) elongate, subrectangular, anterior margin obviously concave, lateral margins weakly convex.

Body entirely yellowish brown (Fig. 2). Entire body with numerous closely-spaced foveolae, entirely reticulate, with deep bottoms. Antennal scape, outer surface of mandibles and legs with fine dense micropunctures. Body entirely covered with sub-erect hairs. Antennae and legs with dense short decumbent hairs.

Comparative notes: *Syscia chinensis* **sp. nov.** is clearly distinguished from all other species in the genus by Antennae having 10 segments (Fig. 2C).

This new species is most similar to *S. arcodorsa*. In full-face view of the new species, posterior margin of head nearly straight; frontal

carinae short, less than one-third of head length; anterior margin of clypeus weakly convex (Fig. 2A); in lateral view, mesosoma dorsal outline slightly straight (Fig. 2C); petiolar node (excluding sternite) square, slightly equal in length and height (Fig. 2B). Conversely, in full-face view of *S. arcodorsa*, middle part of posterior margin of head slightly concave; frontal carinae slightly long, less than half of the head length; anterior margin of clypeus almost straight (Supp 1. Fig. S6A); in lateral view, mesosoma dorsal outline strongly convex; petiolar node (excluding sternite) trapezoidal, slightly longer than high (Suppl 1. Fig. S6C).

Distribution: China (Yunnan).

Habitat: It is a forest ecosystem dominated by tropical monsoon forests, mountain rain forests, wet monsoon evergreen broad-leaved forests, and mountain moss evergreen broad-leaved forests; it is an important component and biological corridor of the "Green Triangle" at the junction of China, Vietnam and Laos. The understory herbs are *Ageratina adenophora* (Spreng.) R. M. King & H. Rob. 1826 and Poaceae plants (Fig. 1). This new species nests in wet soil in an open area of a coniferous and broad-leaved mixed forest at an altitude of 1263m and forages on the ground. Temperature at midday sampling was 25°C and the relative humidity was 40%.

Molecular Phylogenetic Analyses

The phylogenetic trees generated by Bayesian inference and maximum likelihood methods exhibit similar topological structures (Suppl 1. Fig. S11-12). Two specimens of Syscia chinensis sp. nov. (KIZ20230160F and KIZ20230160G), form a separate clade with high support (Bayesian posterior probabilities 1.00; Bootstrap support 100%). The clade nodes of the new species showed weak support when compared with other species in the genus in both tree-building methods, so we cannot determine the exact position of this clade (Fig. 3). Genetic distance to the most closely related species (S. volucris and S. setosa) was 16.90-16.93% (see Suppl 2. Table S4). These patterns support morphological analyses indicating that S. chinensis is a distinct species.



Fig. 3. Maximum likelihood methods phylogenetic tree of *Syscia* species based on COI fragments. Node numbers indicate bootstrap support in maximum-likelihood analyses (values below 70% not shown) (Felsenstein 1985). Note: The scale bar represents the number of nucleotide substitutions per site. A scale bar of 0.1 indicates that a branch length of 0.1 corresponds to an average of 10% nucleotide changes between the sequences compared.



Fig. 4. Antennae segments. (A) S. chinensis sp. nov. (B) S. zhoui Du et al. (C) S. arcodorsa Du et al. (D) S. guizhouensis (Zhou)

5. Antennae with 9 segments (Fig. 4B) (China)...
Syscia zhoui Du et al., 2024
Antennae with 11 segments (Fig. 4C, D).......6

DISCUSSION

The ant genus Syscia Roger, 1861 is a cryptobiotic group of the subfamily Dorylinae Leach, 1815. Up to now, it is the only doryline genus with a disjunct distribution between the Old and New World. The molecular phylogenetic tree of the subfamily Dorylinae made by Borowiec (2019) showed that Syscia is in the middle group of the subfamily's evolutionary development. The number of antennal segments is often not fixed among genera of the subfamily Dorylinae, and there is some variation in the number of antennal segments among different species of the same genus (e.g., Cerapachys Smith, 1857 9, 11 or 12; *Dorylus* Fabricius, 1793 8, 9, 11 or 12; Yunodorylus Xu, 2000 11-12; Ooceraea Roger, 1862 8-11). Syscia chinensis, a new species with 10 antennal segments found in the Old World, is in line with expectations and adds to our knowledge of the species diversity of this genus.

Our phylogenetic analysis, based on COI sequences, supports the distinctiveness of Syscia chinensis from other Syscia species. While COI-based phylogenies may be limited by potential homoplasy or incomplete lineage sorting (Hebert et al. 2003; Pons et al. 2006), the observed genetic distance between S. chinensis and known species (e.g., 16.9%, see Suppl 2. Table S4) exceeds typical intraspecific variation in ants (Jansen and Savolainen 2020), aligning with clear morphological differences. Specifically, S. chinensis is diagnosable by antennae having 10 segments, which is absent in all other Syscia species. These congruent molecular and morphological divergences strongly support the recognition of S. chinensis as a new species.

During our survey, only a small number of workers were found (no queen and male). So we need to conduct more extensive surveys to determine the distribution range of the new species. Due to the incomplete survey of China, given the complexity and heterogeneity of China's geography and climate, there are more hidden and undescribed *Syscia* species waiting to be discovered.

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REFERENCES

- AntWeb, 2024. AntWeb, California Academy of Sciences, San Francisco, California, USA. http://www.antweb.org/ [accessed 1 October 2024]
- Antwiki, 2024. AntWiki, <https://www.antwiki.org/>, retrieved on 1 October 2024.
- Aswaj P, Sahanashree R, Udayakantha WS, Aniruddha M and Priyadarsanan DR, 2021. Two new species of doryline ants (Hymenoptera, Formicidae) with 11-segmented antennae from India. ZooKeys 1056:59-72. 10.3897/ zookeys.1056.68722
- Bingham CT, 1903. The Fauna of British India, Including Ceylon and Burma. Hymenoptera, Vol. II. Ants and Cuckoo-wasps. Taylor and Francis, London, 506 pp. <u>https://doi.org/10.5962/bhl.</u> <u>title.100740</u>
- Bolton B, 2024. An online catalog of the ants of the world. https://antcat.org [Accessed 6 June 2024]

- Borowiec ML, 2016. Generic revision of the ant subfamily Dorylinae (Hymenoptera, Formicidae). ZooKeys 608: 1–280. <u>https://</u> doi.org/10.3897/zookeys.608.9427
- Borowiec ML, 2019. Convergent evolution of the army ant syndrome and congruence in bigdata phylogenetics. *Systematic Biology* 68, 642–656. doi:10.1093/sysbio/syy088
- Brady SG, Fisher BL, Schultz TR and Ward PS, 2014. The rise of army ants and their relatives: diversification of specialized predatory doryline ants. *BMC Evolutionary Biology* 14 (93): 1–14. <u>https://doi.org/10.1186/1471-2148-14-93</u>
- Brown WL, 1975. Contributions toward a reclassification of the Formicidae. V. Ponerinae, tribes Platythyreini, Cerapachyini, Cylindromyrmecini, Acanthostichini, and Aenictogitini. Search. Agriculture (Ithaca, New York) 5 (1): 1–115.
- Dalla Torre KW, 1893. Catalogus Hymenopterorum hucusque descriptorum systematicus et synonymicus. Vol. 7. Formicidae (Heterogyna). W. Engelmann, Leipzig. <u>https://</u> doi.org/10.5962/bhl.title.10348
- Donisthorpe H, 1943. A list of the type-species of the genera and subgenera of the Formicidae. [concl.]. Annals and Magazine of Natural History (11) 10: 721-737. <u>https://doi.org/10.1080/00222934308527388</u>
- Du CC, Xu ZH and Chen ZL, 2024. Taxonomic account of the ant genus *Syscia* Roger, 1816 (Hymenoptera, Formicidae) from Asia, with descriptions of two new species from China. *European Journal of Taxonomy* 930:157-181. https://doi.org/10.5852/ejt.2024.930.2491
- Emery C, 1902. Note mirmecologiche. *Rendiconti delle* Sessioni della Reale Accademia delle Scienze dell'Istituto di Bologna (n.s.) 6: 22–34.
- Emery C, 1911. Hymenoptera. Fam. Formicidae. Subfam. Ponerinae. Genera Insectorum 118: 1–125.
- Felsenstein J,1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39(4): 783-791
- Folmer O, Black M, Hoeh W, Lutz R and Vrijenhoek R, 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3(5): 294–299.
- Forel A, 1900. Les Formicides de l'Empire des Indes et de Ceylan. Part VII. *Journal of the Bombay Natural History Society* 13: 303–332.

- Forel A, 1917. Cadre synoptique actuel de la faune universelle des fourmis. *Bulletin de la Société Vaudoise des Sciences Naturelles* 51: 229– 253.
- Hebert PDN, Cywinska A, Ball SL and Waard JR, 2003. Biological identifications through DNA barcodes. Proceedings of the Royal Society of London: Series B, Biological Sciences 270 (1512): 313–321. <u>https://doi.org/10.1098/</u> rspb.2002.2218
- Jaitrong W, Wiwatwitaya D and Yamane S, 2020. First record of the ant genus *Syscia* Roger, 1861 (Hymenoptera: Formicidae) from Thailand, with descriptions of two new species. *Far Eastern Entomologist* 411: 1–9. <u>https://doi.org/10.25221/fee.411.1</u>
- Jansen G and Savolainen R, 2010. Molecular phylogeny of the ant tribe Myrmicini (Hymenoptera: Formicidae). Zoological Journal of the Linnean Society 160:482-495.
- Kempf WW, 1972. Catálogo abreviado das formigas da região Neotropical. *Studia Entomologica* 15: 3–344.
- Letunic I, and Bork P, 2021. Interactive tree of life (iTOL) v5: an online tool for phylogenetic tree display and annotation. *Nucleic Acids Res* 49 (W1): W293-W296. <u>https://doi.org/10.1093/</u> <u>nar/gkab301.</u>
- Longino JT and Branstetter MG, 2021. Integrating UCE phylogenomics with traditional taxonomy reveals a trove of New World Syscia species (Formicidae: Dorylinae). Insect Systematics and Diversity 5 (2): 1–51. <u>https://doi.org/10.1093/isd/ixab001</u>
- Nei M and Kumar S, 2000. *Molecular Evolution and Phylogenetics*. Oxford University Press, New York.
- Pons J, Barraclough TG, Gomez-Zurita J, Cardoso A, Duran DP, Hazell S, Kamoun S, Sumlin WD and Vogler AP, 2006. Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology* 55: 595-609.
- Roger J, 1861. Die Ponera-artigen Ameisen (Schluss). Berliner Entomologische Zeitschrift 5: 1–54.
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, et al., 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61(3), 539–542. <u>https:// doi: 10.1093/sysbio/sys029</u>
- Tamura K, Stecher G and Kumar S, 2021. MEGA 11: Molecular Evolutionary Genetics Analysis Version 11. *Molecular Biology and Evolution*. <u>https://doi.org/10.1093/molbev/msab120.</u>

- Thompson JD, Gibson TJ and Higgins DG, 2002. Multiple sequence alignment using ClustalW and ClustalX. Current Protocols in Bioinformatics 00(1): 2.3.1–2.3.22. <u>https://</u> doi.org/10.1002/0471250953.bi0203s00
- Wheeler WM, 1902. An American *Cerapachys*, with remarks on the affinities of the Cerapachyinae. *Biological Bulletin (Woods Hole)* 3: 181–191. https://doi.org/10.2307/1535872
- Wheeler WM, 1910. Ants: Their Structure, Development and Behavior. Columbia University Press, New York. <u>https://doi.org/10.5962/bhl.</u> <u>title.1937</u>
- Wheeler WM, 1922. Ants of the American Museum Congo expedition : a contribution to the myrmecology of Africa. *Bulletin of the American Museum of Natural History*: 45: 1–1139.
- Xu ZH, 2002. A Study on the Biodiversity of Formicidae Ants of Xishuangbanna Nature Reserve. Yunnan Science and Technology Press, Kunming, 181 pp.

- Yamane S and Mizuno R, 2024. Three new species of the ant genera *Ooceraea* and *Syscia* (Hymenoptera: Formicidae: Dorylinae) from Sabah, Borneo. *Asian Myrmecology* 17: e017004:1-14.
- Zhang D, Gao F, Jakovli'c I, Zou H, Zhang J, Li WX and Wang GT, 2020. PhyloSuite: An integrated and scalable desktop platform for streamlined molecular sequence data management and evolutionary phylogenetics studies. *Molecular Ecology Resources* 20, 348–355.
- Zhou SY, 2006. Formicidae. In: Li Z.Z. & Jin D.C. (eds) Insects from Fanjingshan Landscape: 579–589. Guizhou Science and Technology Publishing House, Guiyang.