



Description of *Trypoxylon sicklum* sp. nov. from Vietnam and a key to species in the *Trypoxylon fulvocollare* group (Hymenoptera, Crabronidae)

Phong Huy Pham^{‡,§}, Alexander V. Antropov^{||}, Hieu Van Nguyen[¶]

‡ Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet, Cau Giay, Hanoi, Vietnam

§ Graduate University of Science and Technology, Vietnam Academy of Science and Technology, Hanoi, Vietnam

| Zoological Museum of Moscow, Lomonosov State University, Bolshaya Nikitskaya str. 2, Moscow, 125009, Moscow, Russia

¶ Faculty of Biology and Agricultural Engineering, Hanoi Pedagogical University 2, 32 Nguyen Van Linh Street, Xuan Hoa, Phuc Yen, Vinh Phuc, Vietnam

Corresponding author: Phong Huy Pham (phong.wasp@gmail.com)

Academic editor: Silas Bossert

Received: 17 Oct 2023 | Accepted: 24 Apr 2024 | Published: 21 May 2024

Citation: Pham P, Antropov AV, Nguyen H (2024) Description of *Trypoxylon sicklum* sp. nov. from Vietnam and a key to species in the *Trypoxylon fulvocollare* group (Hymenoptera, Crabronidae). Biodiversity Data Journal 12: e114333. <https://doi.org/10.3897/BDJ.12.e114333>

ZooBank: [urn:lsid:zoobank.org:pub:0BD79933-47E3-4FB9-880D-2310353CEFE5](https://www.zoobank.org/pub:0BD79933-47E3-4FB9-880D-2310353CEFE5)

Abstract

Background

Trypoxylon Latreille, 1796 (Hymenoptera, Crabronidae) consists of 633 known species worldwide and the genus is divided into numerous species groups. In Vietnam, 19 species of *Trypoxylon* have been recorded to date. In this study, a new species, *Trypoxylon sicklum* Pham and Antropov sp. nov. is described and illustrated from Vinh Phuc Province, Vietnam. The new species is the second member of the *Trypoxylon fulvocollare* species group. A key to species in the *Trypoxylon fulvocollaris* group is presented.

New information

Trypoxylon sicklum Pham and Antropov sp. nov., is described as a new species and is the second member of the *Trypoxylon fulvocollare* species group. A key to species in the *Trypoxylon fulvocollaris* group is presented.

Keywords

Crabronidae, new species, taxonomy, *Trypoxylon*, Vietnam

Introduction

Trypoxylon is worldwide in distribution with 633 described species. These wasps are solitary members of the family Crabronidae (Sann et al. 2018, Pulawski 2023). The genus consists of two subgenera, *Trypoxylon* and *Trypargilum*. Whereas the former, consisting of 544 species, is distributed in the Ethiopian, Palearctic, Oriental and Australian Regions, the latter, consisting of 89 species, is distributed only in the Neotropical and Nearctic Regions. Based on external morphological characters and male genitalia structures, *Trypoxylon* is divided into numerous species groups (Richards 1934, Tsuneki 1978a, Tsuneki 1981, Antropov 1994, Antropov 2003, Antropov 2011).

In Vietnam, Pham et al. (2015) and Pham and Antropov (2021) recorded seven *Trypoxylon* species. Recently, Pham et al. (2023) have recorded 14 species in North Vietnam, 12 of them being new records. Altogether, 19 species of the genus have been recorded for the country. During a study course of Hymenoptera in 2023 in Vinh Phuc Province, we collected three specimens of a *Trypoxylon* species. After a closer examination of these specimens, we conclude that they represent a new species and describe it here.

Tsuneki (1981) defined the *Trypoxylon fulvocollare* species group, based on male genitalia characters including the shoulder of the penis valve being almost horizontal; paramere bifurcate at apex; apical lobes of paramere appropriately similar in length; bifurcation deep, reaching top of inner expansion of basiparamere; ventral one of apical lobes of paramere much broader and slightly shorter than dorsal lobe; inner margin of ventral lobe of paramere and that of outer area of basiparamere in a line running straight. The species group previously consisted of a single species, *T. fulvocollare* Cameron 1904 (Tsuneki 1978b, Tsuneki 1979, Tsuneki 1981, Pulawski 2023). The new species described here belongs to this species group as it exhibits the above-mentioned characters, thus representing a second species. Lastly, we present a key to the two species of the *Trypoxylon fulvocollare* group.

Materials and methods

Sampling was carried out using trap nests, which were placed on horizontal branches, 1 - 2.5 m from the ground with their entrances orientated south and north. The trap nests were maintained in the field from 15 to 20 days. Trap nests occupied by *Trypoxylon* were collected and wasps were reared under laboratory conditions. Adult wasps that emerged from these trap nests were kept, euthanised with a killing jar charged with ethyl acetate, pinned and described with the aid of a light stereomicroscope (Nikon SMZ745). Photographic images were taken using a Nikon SMZ800N microscope camera. Morphological terms used in the text follow Bohart and Menke (1976) and Tsuneki (1979).

Specimens examined including the holotype and the paratype of the new species are deposited in the Institute of Ecology and Biological Resources (IEBR), Vietnam Academy of Science and Technology, Ha Noi, Vietnam.

The following abbreviations are used in the text:

- A(x): Antennal joint, x being the joint number
- ASR: Antennal socket rim
- PAF: Furrow between ASR and SAT
- SAT: Supraantennal tubercle
- G(g): Gastral segment, g being the gastral number.

Taxon treatment

Trypoxylon sicklum Pham & Antropov sp. nov.

- ZooBank [27CFAE77-EF91-44FE-8BFC-DDA9D2C6811B](https://doi.org/10.2777/27CFAE77-EF91-44FE-8BFC-DDA9D2C6811B)

Materials

Holotype:

- a. occurrenceID: 4CFA42D6-014D-520D-8674-71C7C28468D8
- b. scientificName: Hymenoptera, Crabronidae, *Trypoxylon sicklum* Pham & Antropov, sp. nov.; higherClassification: Insect; kingdom: Animalia; order: Hymenoptera; family: Crabronidae; taxonRank: species; genus: *Trypoxylon*; specificEpithet: *sicklum*; scientificNameAuthorship: Pham & Antropov, 2023; country: Vietnam; stateProvince: Vinh Phuc; locality: Me Linh Station for Biodiversity, Ngoc Thanh commune, Phuc Yen City; locationRemarks: Vinh Phuc: Me Linh Station for Biodiversity, Ngoc Thanh commune, Phuc Yen City, 5 July 2023, trap nests; georeferenceProtocol: label; samplingProtocol: trap nests; eventDate: 05/07/2023; individualCount: 1; sex: female; lifeStage: adult; catalogNumber: VP202307050001; recordNumber: 2023; recordedBy: Phong Huy Pham; occurrenceStatus: Present; disposition: in collection; identifiedBy: Phong Huy Pham; dateIdentified: 2023; language: en; collectionCode: Insects; basisOfRecord: PreservedSpecimen; occurrenceID: C01CD1AE-2EB1-574F-AD84-2933E5988EF7
- c. scientificName: Hymenoptera, Crabronidae, *Trypoxylon sicklum* Pham & Antropov, sp. nov.; higherClassification: Insect; kingdom: Animalia; order: Hymenoptera; family: Crabronidae; taxonRank: species; genus: *Trypoxylon*; specificEpithet: *sicklum*;

scientificNameAuthorship: Pham & Antropov, 2023; country: Vietnam; stateProvince: Vinh Phuc; locality: Me Linh Station for Biodiversity, Ngoc Thanh commune, Phuc Yen City; locationRemarks: Vinh Phuc: Me Linh Station for Biodiversity, Ngoc Thanh commune, Phuc Yen City, 5 July 2023, trap nests; georeferenceProtocol: label; samplingProtocol: trap nests; eventDate: 05/07/2023; individualCount: 1; sex: male; lifeStage: adult; catalogNumber: VP202307050002; recordNumber: 2023; recordedBy: Phong Huy Pham; occurrenceStatus: Present; disposition: in collection; identifiedBy: Phong Huy Pham; dateIdentified: 2023; language: en; collectionCode: Insects; basisOfRecord: PreservedSpecimen; occurrenceID: E5E0EAC9-0776-5013-96DA-D8A2FBEB32FB

Paratype:

- a. scientificName: Hymenoptera, Crabronidae, *Trypoxylon sicklum* Pham & Antropov, sp. nov.; higherClassification: Insect; kingdom: Animalia; order: Hymenoptera; family: Crabronidae; taxonRank: species; genus: *Trypoxylon*; specificEpithet: *sicklum*; scientificNameAuthorship: Pham & Antropov, 2023; country: Vietnam; stateProvince: Vinh Phuc; locality: Me Linh Station for Biodiversity, Ngoc Thanh commune, Phuc Yen City; locationRemarks: Vinh Phuc: Me Linh Station for Biodiversity, Ngoc Thanh commune, Phuc Yen City, 5 July 2023, trap nests; georeferenceProtocol: label; samplingProtocol: trap nests; eventDate: 05/07/2023; individualCount: 1; sex: male; lifeStage: adult; catalogNumber: VP202307050003; recordNumber: 2023; recordedBy: Phong Huy Pham; occurrenceStatus: Present; disposition: in collection; identifiedBy: Phong Huy Pham; dateIdentified: 2023; language: en; collectionCode: Insects; basisOfRecord: PreservedSpecimen; occurrenceID: 1F767E5C-E000-55DC-B815-FF5E4C076137

Description

Female. Body length 14.2 mm, forewing length 10.3 mm.

Colour. Body black with following parts yellow: A1–A4; base of A5; band immediately after apical margin of clypeus; base of mandible; maxillary and labial palps; tegula; pronotal collar; pronotal lobe; fore coxa; base of mid- and hind-coxae; fore- and mid-trochanters ventrally, femora, tibiae, and tarsi; half of base of hind tibia; lateral sides of petiole, broad base of G2 and G3; apical bands of G1–G5. Following parts ferruginous: apical margin of clypeus; apical two-thirds of mandible; two-thirds of apex of A5, A6–A12; hind trochanter, femur, half apex of tibia and tarsi; half base of petiole dorsally; sides and ventral surface of G6. Veins of wings yellow to brown.

Vestiture. Golden on head and mesosoma, white on metasoma.

Head (Fig. 1A, B). In anterior view, nearly round, width about 1.2× height, its sides roundly convergent below; apex of clypeus blade-shaped, round apically; mandible without tooth; SAT moderately raised with short median carina; ASR moderately high with three distinct carinae; PAF shallow, flat-bottomed; ocelli round and distinctly protruded; frons with rather narrow furrow medially and small punctures, sparse on median area and dense on lateral sides; vertex depressed below level of upper eye margin, with small sparse punctures; occipital carina complete; relative lengths of A1: A2: A3: A4: A5 = 27: 14: 48: 28: 28, respectively; relative lengths of minimum interocular distance at the vertex: Ocellocular distance (distance between inner margin of eye and outer margin of hind ocellus): Ocellar diameter: Postocellar distance

(distance between inner margins of hind ocelli) = 37: 3: 12: 7, respectively; ratio of minimum interocular distance at the vertex: minimum interocular distance at base of clypeus = 1.

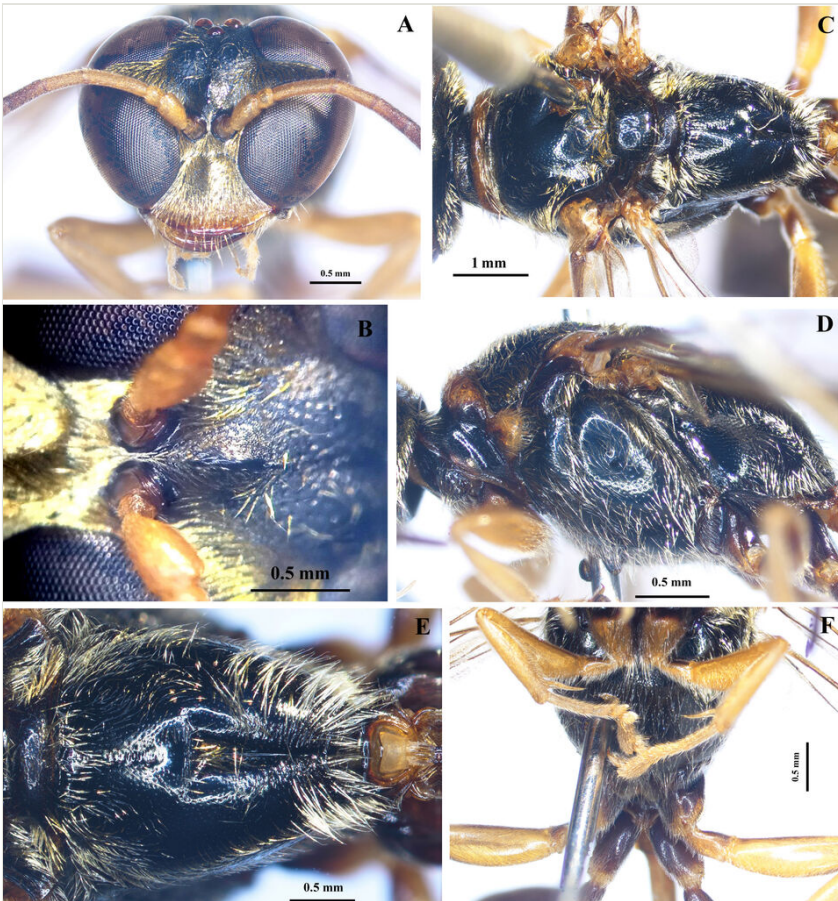


Figure 1. [doi](#)

Trypoxylon sicklum Pham & Antropov sp. nov., holotype, female. **A** head, frontal view; **B** frons; **C** mesosoma, dorsal view; **D** mesosoma, lateral view; **E** propodeum, dorsal view; **F** mesosoma, ventral view.

Mesosoma (Fig. 1C-F, Fig. 2A). Pronotal collar with anterior part moderately swollen posteromedially, posterior part discoloured; pronotal lamella triangularly protruded, with apical angle approximately 150°; subalar area of mesopleuron with pent-roofed structure distinctly developed; mesoscutum, scutellum, metanotum, propodeum with sparse, fine, small punctures; mesopleuron with rather dense punctures; propodeum without lateral carina, with median groove dorsally, shallow on basal half and deep on apical half, posterior surface with a series of horizontal striae and median grooves conspicuously deep; gastral socket rim simple, nearly roundly elevated. Wings hyaline; forewing with stigma as long as prestigma.

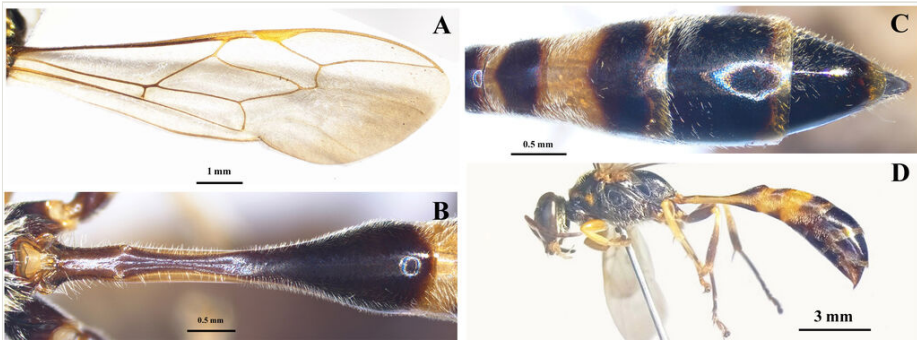


Figure 2. [doi](#)

Trypoxylon sicklum Pham & Antropov sp. nov., holotype, female: **A** fore wing; **B** petiole; **C** metasoma, dorsal view; **D** habitus, lateral view.

Metasoma (Fig. 2B-D). Shiny, with very sparse micropunctures on petiole and G2–G5; petiole flask-shaped, length about 4× its apical width and about 1.3× that of G2 and G3 combined, with its apex more highly protruding than base of G2; tergum of G6 rounded apically, rugose basally, impunctate, its apex slightly curved upwards.

Male. Body length 12.6 mm, forewing length 9.1 mm.

Structures as in female, but differing as follows:

Colour. A1–A7 yellow; A8–A13, half apex of clypeus, maxillary and labial palps ferruginous, half apex of mandible black.

Head (Fig. 3A-C). A3 shorter than A1 and A2 combined, but longer than A4, A5; relative length of A1: A2: A3: A4: A5 = 19: 9: 20: 15: 15; A13 as long as A9–A12 combined; relative length of minimum interocular distance at the vertex: Ocellocular distance: Ocellar diameter: Postocellar distance = 32: 5: 8: 6, respectively.

Genitalia (Fig. 4D-F). Brownish-yellow, except apical part of sickle black. Penis valve with shoulder, sickle and apical part; shoulder horizontal; sickle conspicuously curved, with its apex distinctly pointed; apical part moderately curved; paramere with two lobes at apex (namely, ventral and dorsal lobes), their length about equal, ventral lobe much broader than dorsal lobe; furrow between two lobes deep, reaching apex of inner expansion of basiparamere; inner margin of ventral lobe and inner margin of outer area of basiparamere in a line moderately curved medially. Dorsal lobe with some long, erect setae apically; ventral lobe with 5–6 long, erect setae at apex, subapical part with several sparse, erect setae along outer margin.

Diagnosis

The new species runs close to *T. shakha* Tsuneki, 1979 in a key of *Trypoxylon* of the Indian subcontinent and Southeast Asia (Tsuneki 1979). In *T. shakha* and in the newly-described species, the females display the following characters: vertex depressed

below level of upper eye margin; PAF flat-bottomed; occipital carina complete; propodeum without lateral carinae, dorsal area with furrow; frons, mesoscutum, scutellum, metanotum and propodeum with small sparse punctures. Following parts with yellow integument: A1–A4, pronotal collar, fore- and mid-legs, except broad base of mid-coxa, tergal base of G2–G4, apical bands of G3–G5. Vestiture golden on head and mesosoma. Females of the new species differ from those of *T. shakha* as follows: Clypeus round apically (in *T. shakha*, clypeus not round apically, with median margin highly protruded and truncated apically); PAF shallow (in *T. shakha*, PAF deep); SAT dorsally with medial carina short, not enlarged, not broadly excavated (in *T. shakha*, SAT dorsally with medial carina enlarged into a smooth and round area and broadly excavated); ASR moderately raised (in *T. shakha*, ASR highly raised, bicarinate on apex); vestiture white on metasoma (in *T. shakha*, vestiture golden on metasoma).

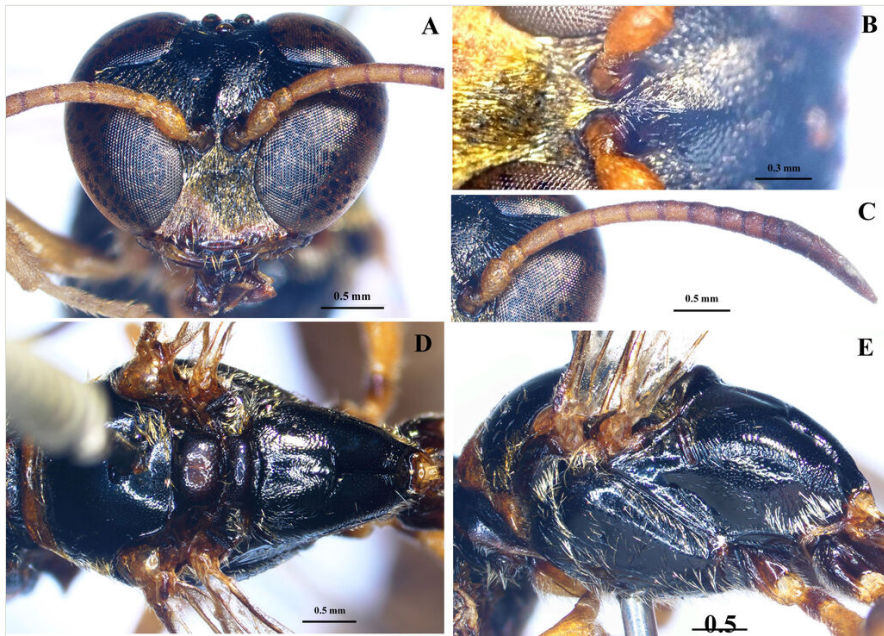


Figure 3. [doi](#)

Trypoxylon sicklum Pham & Antropov sp. nov., paratype, male. **A** head, frontal view; **B** frons; **C** antenna; **D** mesosoma, dorsal view; **E** mesosoma, lateral view.

Metasoma (Fig. 4A-C). Petiole with length 3.5× its apical width.

Etymology

The specific name of this new species refers to the sickle shape of the penis valve.

Distribution

Vietnam: Vinh Phuc Province.

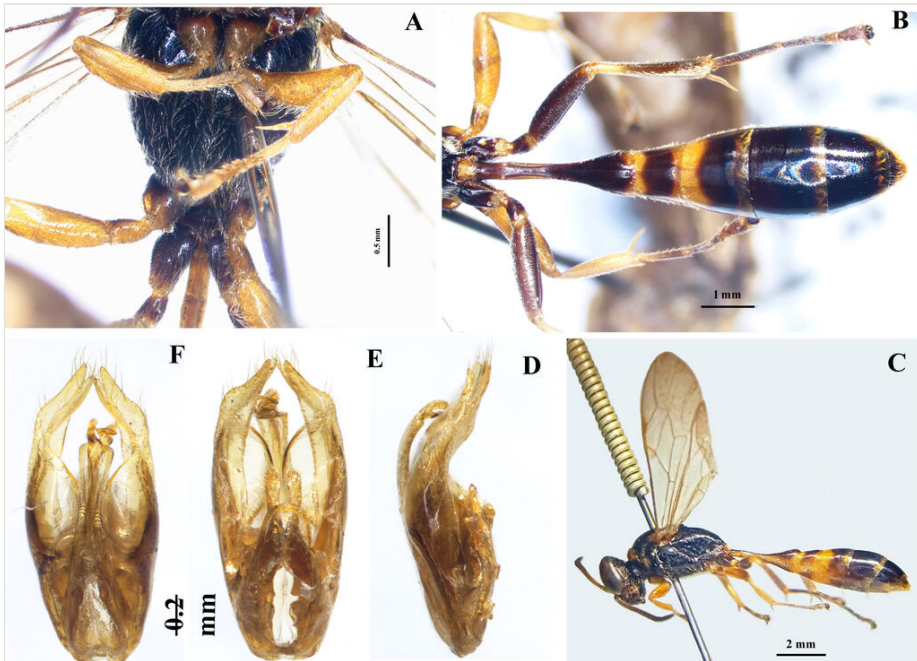


Figure 4. [doi](#)

Trypoxylon sicklum Pham & Antropov sp. nov., paratype, male and genitalia. **A** mesosoma, ventral view; **B** metasoma, dorsal view; **C** habitus, lateral view; **D** genitalia, lateral view; **E** genitalia, ventral view; **F** genitalia, dorsal view.

Identification keys

Key to species in the *Trypoxylon fulvocollare* group, females

1	Vertex depressed much below level of upper eye margins; distance between inner margins of hind ocelli equal to distance between inner margin of eye and outer margin of hind ocellus; propodeum with lateral carinae, dorsal area without lateral furrows; petiole as long as G2 and G3 combined	<i>T. fulvocollare</i> Cameron, 1904
–	Vertex depressed moderately below level of upper eye margins; distance between inner margins of hind ocelli 2× distance between inner margin of eye and outer margin of hind ocellus; propodeum without lateral carinae, dorsal area with lateral furrows; petiole much longer than G2 and G3 combined	<i>T. sicklum</i> sp. nov. Pham & Antropov

Key to species in the <i>Trypoxylon fulvocollare</i> group, males		
1	A13 as long as A8–A12 combined; petiole with length 4–5× its apical width; subapical part of ventral lobe of paramere with rather dense, erect setae; sickle brownish-yellow, lightly to moderately curved; inner margin of ventral lobe and that of outer area of basiparamere in a line straight or slightly curved medially	<i>T. fulvocollare</i> Cameron, 1904
–	A13 shorter than A8–A12 combined; petiole with length 3.5× its apical width; subapical part of ventral lobe of paramere with some long, erect setae; sickle conspicuously curved, with apical part black; inner margin of ventral lobe and that of outer area of basiparamere in a line moderately curved medially	<i>T. sicklum</i> sp. nov. Pham & Antropov

Discussion

As the male of *T. shaka* is unknown, it has not been placed in any *Trypoxylon* species group. External morphological characters of females of *T. shakha* are similar to those of *T. sicklum* sp. nov., suggesting that *T. shakha* may be a member of the *T. fulvocollare* species group. To clear this matter, future morphological studies on males of *T. shaka* are required.

Trypoxylon sicklum sp. nov. was found in a montane forest habitat, about 350 m in elevation, in Vinh Phuc Province of Vietnam. The wasp used two trap nests for its nesting site. Most *Trypoxylon* species construct their nests in pre-existing cavities, such as holes in wood, bamboo and other plant stems and in abandoned mud nests of other wasps. Use of trap nests is common in *Trypoxylon* and has been reported for various species, such as *T. carinatum*, *T. frigidum*, *T. kolazyi*, *T. clavatum*, *T. collinum*, *T. lactitarse* and *T. tridentatum* (see Krombein (1967)); *T. deceptorium*, *T. clavicerum*, *T. figulus* and *T. scutatum* (see Kazenas (2001)); and *T. bicolor* (see Vicens et al. (2022)). In contrast, several species in the genus (the subgenus *Trypargilum*) construct their nests with mud and are, thus, called pipe-organ wasps, for example *T. monteverdeae* (see Brockmann (1992)) and *T. politum* (see Brockmann and Grafen (1992)).

Acknowledgements

The authors thank Dr. Wojciech J. Pulawski, California Academy of Sciences, San Francisco, USA for providing the respective literature and Mrs. Khuc Thi Ut for her help in collecting voucher specimens. We are grateful to Dr. Silas Bossert, subject editor, Dr. Richard Zack and an anonymous reviewer for their valuable and helpful comments on the manuscript. This research is funded by the Vietnam Ministry of Education and Training and Hanoi Pedagogical University 2 under grant number B.2021-SP2-07 to the third author. Fieldwork was financed by the Biodiversity Conservation Organization IDEA WILD, Fort Collins, U.S.A. through funding to the first author.

Author contributions

The authors confirm their contribution in the paper as follows: Ph.H.P. conceived the ideas, designed the methodology, collected the data and led the writing of the manuscript; H.V.N collected and analysed the data; A.V.A. supported writing the manuscript and edited the text. All authors contributed critically to the drafts and gave final approval for publication.

References

- Antropov AV (1994) Four new species of the digger wasp genus *Trypoxylon* Latreille (Hymenoptera, Sphecidae) of the Palaearctic and Oriental Regions, with taxonomic notes on some others previously described. *Russian Entomological Journal* 3 (1-2): 123-133.
- Antropov AV (2003) On the occurrence of *Trypoxylon attenuatum* F. Smith, 1951 (Hymenoptera: Crabronidae: Trypoxylini) in North America. *Russian Entomological Journal* 11 (4): 437-439.
- Antropov AV (2011) Order Hymenoptera, family Crabronidae. Genera *Trypoxylon*, *Pseudomicroides* and *Belomicroides*. *Arthropod Fauna of the UAE* 4: 609-629.
- Bohart RM, Menke AS (1976) Sphecid wasps of the world, a generic revision. University of California Press <https://doi.org/10.1525/9780520309548>.
- Brockmann H (1992) Male behavior, courtship and nesting in *Trypoxylon* (*Trypargilum*) *monteverdeae* (Hymenoptera: Sphecidae). *Journal of the Kansas Entomological Society* 65: 66-84.
- Brockmann HJ, Grafen A (1992) Sex ratios and life-history patterns of a solitary wasp, *Trypoxylon* (*Trypargilum*) *politum* (Hymenoptera: Sphecidae). *Behavioral Ecology and Sociobiology* 30: 7-27.
- Cameron P (1904) Descriptions of new species of aculeate and parasitic Hymenoptera from Northern India. *Annals and Magazine of Natural History (Series)* 13: 211-233. <https://doi.org/10.1080/00222930408678900>
- Kazenas V (2001) Фауна и биология роющих ос Казахстана и Средней Азии. [Fauna i biologiya royushchikh os (Hymenoptera, Sphecidae) Kazakhstana i Sredney Azii = Fauna and biology of sphecid wasps (Hymenoptera, Sphecidae) of Kazakhstan and Central Asia]. Kazgos INTI, Almaty, 333 pp.
- Krombein KV (1967) *Trap-nesting wasps and bees: life histories, nests, and associates*. Smithsonian Press, Washington D.C., 570 pp.
- Pham PH, Girish Kumar P, Danilov Y (2015) Distributional checklist of sphecid wasps (Hymenoptera, Ampulicidae, Sphecidae, Crabronidae) from Vietnam. *Linzer Biologische Beiträge* 47 (2): 1581-1599.
- Pham PH, Antropov A (2021) Contributions to the knowledge of the spheciformes fauna (Hymenoptera: Ampulicidae, Crabronidae, Sphecidae) from Vietnam. *Russian Entomological Journal* 30 (3): 314-322. <https://doi.org/10.15298/rusentj.30.3.09>
- Pham PH, Nguyen A, Antropov A (2023) New records of species of the genus *Trypoxylon* Latreille, 1796 (Hymenoptera: Crabronidae) from northern Vietnam. *Russian Entomological Journal* 32 (1): 58-67. <https://doi.org/10.15298/rusentj.32.1.07>

- Pulawski W (2023) Number of species in Sphecidae (sensu lato). https://researcharchive.calacademy.org/research/entomology/entomology_resources/hymenoptera/sphecidae/genera/Trypoxylon.pdf. Accessed on: 2023-5-05.
- Richards OW (1934) The American species of the genus *Trypoxylon* (Hymenopt., Sphecoidea). Transactions of the Royal Entomological Society of London 82 (2): 173-362. <https://doi.org/10.1111/j.1365-2311.1934.tb00033.x>
- Sann M, Niehuis O, Peters RS, Ch M, Kozlov A, Podsiadlowski L, Bank S, Meusemann K, Misof B, Ch B, Ohl M (2018) Phylogenomic analysis of Apoidea sheds new light on the sister group of bees. BMC Evolutionary Biology 18 (71): 1-15.
- Tsuneki K (1978a) Studies on the genus *Trypoxylon* Latreille of the Oriental and Australian Regions (Hymenoptera, Sphecidae). I. Group of *Trypoxylon scutatum* Chevrier, with some species from Madagascar and the adjacent islands. Special Publications of the Japan Hymenopterists Association 7: 1-87.
- Tsuneki K (1978b) Studies on the genus *Trypoxylon* Latreille of the Oriental and Australian Regions (Hymenoptera, Sphecidae). II. Revision of the type series of the species described by F. Smith, P. Cameron, C.G. Nurse, W. H. Ashmead, R.E. Turner and O.W. Richards. Special Publications of the Japan Hymenopterists Association 8: 1-84.
- Tsuneki K (1979) Studies on the genus *Trypoxylon* Latreille of the Oriental and Australian Regions (Hymenoptera, Sphecidae). III. Species from the Indian subcontinent including Southeast Asia. Special Publications of the Japan Hymenopterists Association 9: 1-178.
- Tsuneki K (1981) Tentative grouping of the *Trypoxylon* species based upon the structure of the male genital organs with appendix of the distribution table (Hymenoptera, Sphecidae). Special Publications of the Japan Hymenopterists Association 18: 1-100.
- Vicens N, Carbonell R, Antropov AV, Bosch J (2022) Nesting biology of *Trypoxylon petiolatum* Smith, 1858 (Crabronidae), a cavity-nesting solitary wasp new to Europe. Journal of Hymenoptera Research 90: 153-171. <https://doi.org/10.3897/jhr.90.78581>