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Nesting biology of *Trypoxylon petiolatum* Smith, 1858 (Crabronidae), a cavity-nesting solitary wasp new to Europe

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Abstract

We report on the discovery of the spider-hunting wasp *Trypoxylon petiolatum* (Crabronidae) nesting in three localities in the Province of Girona (Catalonia, NE Spain) in 2019 and 2021. This species is native to eastern Asia and has not previously been reported from Europe. We provide a detailed description of the species, as well as information on its nest architecture, cocoon shape, the identity of the spiders captured to provision the nests, and mortality rates, including parasitism by a native cleptoparasitic fly (*Amobia signata*, Miltogramminae, Sarcophagidae) and a native parasitoid wasp (*Melittobia acasta*, Eulophidae).

Keywords

Alien species, exotic species, Salticidae, spider-hunting wasp

Introduction

In Europe, ca. 300 Hymenoptera species, mainly of North American and Asian origin, have been recorded as alien (Rasplus et al. 2010). Most of these species are Parasitica wasps (79.5%) and ants (14.5%), with Aculeate wasps and bees representing only 3.4%. However, since the review of Rasplus et al. (2010) the number of exotic

Aculeate wasps and bees detected in Europe has considerably increased (Ornosa et al. 2006; Vereecken and Barbier 2009; Mei et al. 2012; Castro et al. 2013; Mei and Boščík 2016; Schmidt 2017; Bortolotti et al. 2018; Schmid-Egger and Herb 2018; Castro 2019; Mei and Cappellari 2021). Most of these new introductions appear to be related to the expansion of world trade and the exchange of goods across the globe (Bacon et al. 2012).

In this study we report on the discovery of *Trypoxylon petiolatum* (Crabronidae), a cavity-nesting spider-hunting solitary wasp from eastern Asia, nesting in three localities in the province of Girona (Catalonia, NE Spain). As far as we know, this species has not been previously reported from Europe. We provide a detailed description of the species, as well as information on its nesting biology and parasitism by a native cleptoparasitic fly and a parasitoid wasp.

The genus *Trypoxylon* comprises ca. 630 species of solitary wasps (Pulawski 2003; Antropov 2021), distributed worldwide, with the highest diversity in the Oriental and Neotropical regions (Bohart and Menke 1976). Most of them nest in pre-established cavities, but some species (subgenus *Trypargylum*) build free-standing nests attached to rocks and other substrates (Evans and West Eberhard 1973, O'Neill 2001), and a few species have been recorded nesting in cavities underground (Richards 1944). All species provision their nests with paralysed spiders. Eighteen species have been reported from Europe (Antropov 2021).

Methods

The first observations were conducted by R.C. in June 2019 in a farm environment in Beuda (Garrotxa, Girona). One female was observed on a tree stump with drilled holes. At the end of the summer, the stump was isolated throughout the winter within a clear plastic container but no specimens emerged.

The second observations were conducted by N.V. in June 2021 in the city of Girona. Two females were observed on three bundles of bamboo sections placed on a window sill. Each bundle was composed of 25 bamboo sections of various diameters (2–9 mm). One of the nesting females was captured for later identification and seven completed (plugged) nests and one partial nest were recovered. The reed sections were split open and the contents of the nests were analysed and photographed. Unconsumed and partially consumed spiders were put in 70% ethanol for later identification based on Oger (2021) and with the assistance of various colleagues from the Europäischer Spinnentiere Forum (https://forum.arages.de). Some of the nests contained puparia of sarcophagid flies. These were placed in glass vials with a humidified cotton wad to provide moisture and were kept at 24 °C until adult fly emergence. Emerging adults were sacrificed and pinned for later identification by T. Zeegers (Soest, The Netherlands) and T. Pape (Natural History Museum of Denmark, Copenhagen). The nests were reassembled and kept in a holding cage at 24 °C until adult wasp emergence in mid-July. Emerging adults were sacrificed, pinned and identified based on Tsuneki (1979, 1981) and Jeong and Kim (2020). Photographs of relevant body parts were taken and processed using Zerene Stacker software.

The last observations were conducted by N.V. in October 2021 in Bescanó (Girona). One female was observed close to a bundle of bamboo sections (2–9 mm diameter) placed under a porch roof in an isolated farm surrounded by forest. Four complete and one partial nests were recovered from this locality. The contents of these nests was analysed as described above.

Results

Observations

In 19–23 June of 2019, a female *Trypoxylon* with partially red gaster (Fig. 1) was repeatedly observed entering a hole drilled in a tree stump near a farm building in Beuda (Garrotxa, Girona). The specimen caught the attention of the observer because all *Trypoxylon* species from western Europe have black gasters (Antropov 2021). Photographs of the specimen were sent to A.V.A. who pointed out its resemblance to *Trypoxylon petiolatum*, F. Smith, 1858, a species from eastern Asia.

In 11–20 June 2021, two *Trypoxylon* females with partially red gasters were observed nesting in bamboo sections (Fig. 2A) on a window sill facing a landscaped square in the city of Girona. These females were seen sealing nests with mud (Fig. 2A) and carrying paralysed spiders (Fig. 2B). On June 20 one of the females was captured. This female and other individuals reared from nests obtained in this locality were identified as *T. petiolatum*.

On 23 October 2021, a female with partially red gaster was seen carrying a spider close to a bundle of bamboo sections placed under a porch roof in Bescanó (Girona). A partial nest obtained from this locality contained a dead adult female that was identified as *T. petiolatum*.

Trypoxylon petiolatum (12–17 mm body length) is characterized by the elongated (at least 4 times as long as wide), flask-shaped T1 (first metasomal segment), the red colouring of T2 and T3 with dorsal black stains, and the absence of lateral carina in the propodeum. A detailed description of the specimens examined by us is provided in Appendix 1. Females are slightly larger than males (female forewing length: 8.5 (7.8–9.0) mm; male forewing length: 7.4 (7.1–7.7) mm; n = 15 and 3, respectively).

Nest architecture and nesting biology

Nesting activity of two females was observed at the Girona site from 11 to 20 June 2021. On 23 June, we collected seven completed nests and one partial nest at this locality. Four additional completed nests and one partial nest were collected at Bescanó

Figure 1. *Trypoxylon petiolatum* female photographed at Beuda (Girona, NE Spain) in June 2019.

on November 15. The bamboo sections in which the nests were built were 20 cm long with a mean inner diameter of 5.3 mm (range: 4–6 mm). All nests had the same basic structure: a series of cells provisioned with spiders and delimited by mud partitions with some embedded small pebbles (maximum size 0.5 mm), followed by a closing plug, also made of mud mixed with pebbles (Fig. 3). The closing plug of the 11 completed nests was terminal (flush with the nest entrance) in two nests and subterminal (recessed from the nest entrance) in nine nests. Six nests had a vestibular cell between the last provisioned cell and the plug, one nest had two vestibular cells and four had none. No nests had a basal partition at the beginning of the first cell. One nest had an intercalary cell (empty cell between two provisioned cells) and another had two.

During the process of building the cell partitions with the mandibles, the females produced a clearly audible vibration. Cell partition thickness ranged from 1.5 to 6.0 mm (mean: 3.4 mm) and plug thickness from 3–11 mm (mean: 5.3 mm). The length of the provisioned cells ranged from 15 to 30 mm (mean: 20.8 mm) and the length of the vestibular cells from 3 to 15 mm (mean: 9.5 mm).

The number of provisioned cells per nest (considering only completed nests, n = 11) ranged from 3 to 7 (mean: 4.6). We recovered intact spider provisions from 12

Figure 2. *Trypoxylon petiolatum* females nesting in bamboo sections in the city of Girona in June 2020.

cells (mean: 5.2 spiders per cell; range: 1–10). Overall, we collected 115 spiders (all of them Salticidae), of which 69 could be identified to species (Fig. 4). The most abundant species was *Heliophanus apiatus* Simon, 1868, followed by *Icius hamatus* (C. L. Koch, 1846), *Evarcha jucunda* (Lucas, 1846), *Heliophanus tribulosus* (Simon,1868), *Heliophanus kochii* Simon, 1868, and *Salticus mutabilis* Lucas, 1846.

Nineteen adult wasps (16 females, 3 males) emerged from the 38 cells obtained in Girona and we found four live prepupae in the 13 cells obtained in Bescanó (45.1% survival). Eleven cells contained immatures that died from unknown reasons (21% developmental failure). Three nests from Girona contained fly puparia (2, 2 and 4 puparia, respectively) (Figs 3D, 5A). Two adults emerged from these puparia on 5 July and were identified as *Amobia signata* (Meigen, 1824) (Miltogramminae, Sarcophagidae) (Fig. 5B). In all three nests, the puparia were located close to the nest entrance and were preceded by a series of cells with broken partitions and mostly unconsumed spider provisions (Fig. 3D), indicating that the fly larvae had moved from its original cell to the nest entrance. Fourteen cells were destroyed by this cleptoparasitic fly (37% mortality). Five cells from Bescanó nests contained prepupae or larvae attacked by *Melittobia acasta* (Walker, 1839) (38% mortality).

Figure 3. Four *Trypoxylon petiolatum* nests built in reed sections in Girona in June 2021, showing fully grown larvae (**A**), cocoon-spinning larvae (**B**), completed cocoons and an unconsumed spider provision (**C**), one cocoon and three cells destroyed by the cleptoparasitic fly *Amobia signata*, with two puparia close to the nest entrance (**D**).

Figure 4. Cell provisioned with *Heliophanus apiatus* (6 females, 1 male) and *Heliophanus tribulosus* (2 females).

The seven nests from Girona were dissected on 23–27 June. At that time, most larvae had already spun their cocoons but a few were still feeding (Fig. 3). Larval development is illustrated in Fig. 6. The cocoon is composed of a single silky layer that easily collapses upon touch. It has a whitish cream colour. The base of the cocoon is rounded, with a conspicuous thick shiny black meconium, and the apex is characteristically flat (Fig. 6E). The sides are mostly parallel but have a slight constriction close to the base (Fig. 6E). Cocoon length ranges from 14 to 18 mm (mean: 17 mm), considerably less than cell length (mean: 21 mm).

Adults emerged out of the nests from 9 to 17 July. In each of the seven nests, all offspring emerged on the same day. Time from nest completion to adult emergence ranged from 30 to 32 days (mean: 31 days; n = 3 nests). The observation of a female in October strongly suggests the occurrence of at least 3 generations in our area.

Figure 5. Puparia (**A**), habitus (**B**) and head (**C**) of male adult *Amobia signata*.

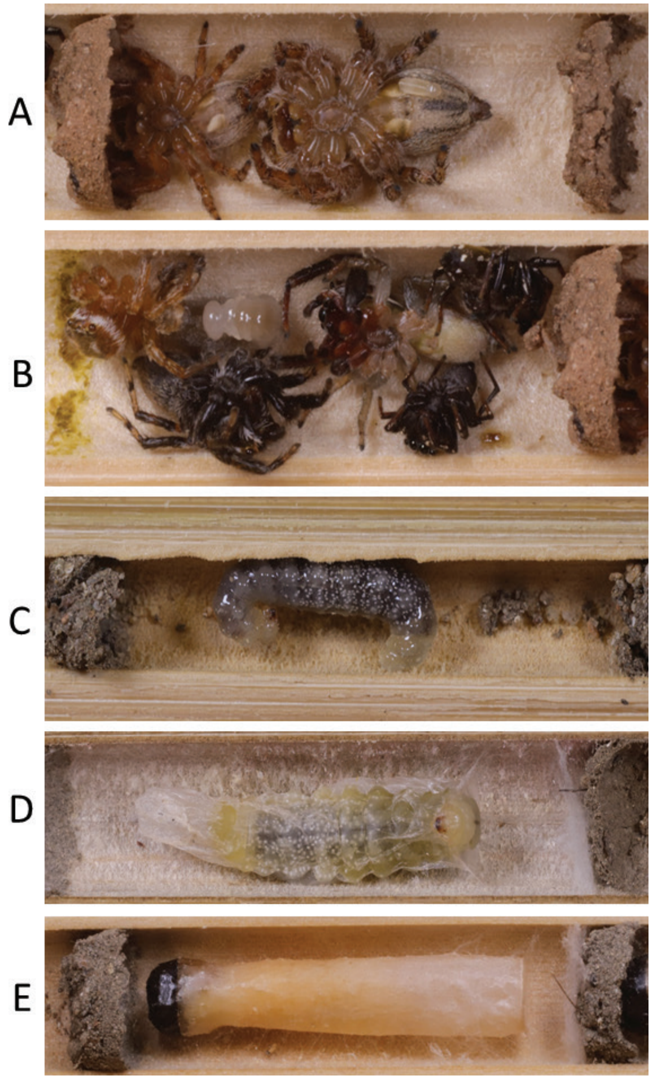

Figure 6. Larval development of *Trypoxylon petiolatum* **A** first instar larva on the abdomen of a spider prey **B** instar 2–3 larva consuming a spider prey **C** post-feeding instar 5 larva **D** larva spinning its cocoon **E** completed cocoon.

Discussion

Trypoxylon petiolatum is native to eastern and southern Asia, including the Indo-Malayan region, the Maldives, Indonesia, Japan, China, Korea and the Philippines (Tsuneki 1981; Jeong and Kim 2020). We found this species for the first time in Europe in three localities distant 10–31 km from each other. We can only speculate as to when, where and how the species was introduced. The nesting stations in Beuda, Bescanó and Girona had been in place since 2014, 2019 and 2020, respectively, but no *T. petiolatum* activity was detected until 2019, 2021 and 2021, respectively. In

September 2021 we analysed 59 *Trypoxylon* nests obtained at another nesting station with bamboo sections in Sant Climent Sescebes (27 km from Beuda). None of the nests was *T. petiolatum*. Five extensive trap-nesting studies have been conducted in Catalonia near Olot (20 km from Beuda; 14 sites), Montseny (43 km from Girona, 42 sites), Garraf (115 km from Girona, 25 sites), Aigüestortes (160 km from Girona, 9 sites) and Lleida (190 km from Girona; 50 sites) in 1991, 2016, 2011–2013, 2008 and 2016, respectively (Barril-Graells et al. 2012; Osorio et al 2015, 2018; Hernández-Castellano 2020; Torné-Noguera et al. 2020). Altogether, these studies produced more than 1000 *Trypoxylon* nests (including *T. figulus* (Linnaeus, 1758), *T. clavicerum* Lepeletier de Saingt Fargeau et Audinet-Serville, 1828, *T. minus* de Beaumont, 1945, *T. scutatum* Chevrier, 1867, and *T. deceptorium* Antropov, 1991), but no nests of *T. petiolatum* were recovered. All this evidence is indicative of a recent introduction localized in the Girona area, but this hypothesis will have to be supported or refuted by future findings of this species. Nests of cavity-nesting wasps and bees can be easily and inadvertently transported in shipments of timber, reeds, and various types of artificial materials with artificial cavities. More than 75% of the alien bee species accidentally introduced out of their distribution ranges are cavity nesters (Russo et al. 2016).

The nesting biology of *T. petiolatum* in its native area of distribution has been described by Barthélémy (2010, 2012), who provides information from Hong Kong and summarises previous studies (Nambu 1966, 1967). Our results are highly coincidental with those of these studies (Table 1).

T. petiolatum females are slightly larger than males. Therefore, according to parental investment theory (Fisher 1958) the primary sex ratio of *T. petiolatum* populations should be slightly biased towards males. Differential mortality between males and females probably explains the strongly biased secondary sex ratios reported in Table 1 (male-biased in Nambu (1966, 1967), and female biased in Barthélémy (2012) and in our study).

We found that *T. petiolatum* females produced a clearly audible vibration when applying mud to the nest partitions. Similar sounds, caused by the wing muscles and transmitted to the mandibles, have been described in other Spheciform wasps when digging or plastering mud to build their nests (Fink et al. 2007; Hansell 2009; Gess and Gess 2014). The shape of the *T. petiolatum* cocoon, with its characteristic sub-basal constriction and the truncated flat apex (Fig. 6E), is noteworthy and may be useful to differentiate *T. petiolatum* nests from those of European congeneric species such as *T. figulus*, *T. clavicerum*, *T. minus*, *T. scutatum* and *T. deceptorium*, in which the apex of the cocoon is more or less rounded. Cocoon shape is a diagnostic trait in North American *Trypoxylon* (Krombein 1967). The high rates of attack by two native parasites, *Amobia signata* and *Melittobia acasta*, are also noteworthy. *Amobia* flies are frequent cleptoparasites of *Trypoxylon* in various parts of the world (Krombein 1967; Kurahashi et al. 1970; Spofford et al. 1989; Coville et al 2000; Oliveira Nascimento and Garófalo 2014; Verves and Protsenko 2020). *Melittobia* are parasitoid wasps that attack a wide range of solitary wasps and bees, as well as their nesting associates (Matthews et al. 2009). *Trypoxylon* spp. are frequent hosts of *Melittobia acasta* in NE Spain (Osorio et al. 2015; Torné-Noguera et al. 2020).

Table 1. Biological traits of *Trypoxylon petiolatum* from nests obtained in Japan (Nambu 1966, 1967), Hong-Kong (Barthélémy 2010) and Girona province (this study).

	Japan	**Hong Kong (n=18 nests)**	**Girona (n= 11 nests)**
Voltinism	One generation	At least four generations	At least three generations
Nesting period of first generation		May	June
Wintering stage	–	–	Prepupa
Nesting substrate	Reeds	Reeds	Reeds
Mean cavity diameter	6.3 mm	4.4 mm	5.2 mm
Nesting material	Mud	Mud	Mud (with small pebbles)
Basal partition	–	Absent-Present	Absent
Intercalary cells	–	0	0–2
Vestibular cell	–	1	0–2
Plug location	–	Terminal	Terminal or subterminal
Mean number of provisioned cells per nest	–	5.5	4.6
Mean length of provisioned cells	–	24.9	21
Mean and range (in parentheses) number of spiders per provision	–	3.9 (2–8)	5.2 (1–10)
% Salticidae prey	> 70%	72%	100%
Timing of egg laying	–	After provision completion	–
Observed secondary sex ratio[†]	2.7 m/f	0.5 m/f	0.2 m/f
% offspring mortality	–	72.0%	56.9%
Nest parasites	Tachinid flies	Unidentified Diptera, *Melittobia* sp.	*Amobia signata*, *Melittobia acasta*
Mean time from egg to adult emergence	32 days	25.5 days	31 days

[†]males/females, considering only offspring that reached the adult stage

Following their introduction, some alien species go extinct, while others maintain small populations around their area of introduction, and others spread rapidly across their new territory and become invasive (Simberloff 1989). The fate of the seemingly incipient *T. petiolatum* population in the Girona area is uncertain. The high percent mortality, including high levels of parasitism by two native species, *A. signata* and *M. acasta* (36.8% and 46.1%, respectively), might suggest a low population growth. However, high mortality rates (up to 70%) are not uncommon in *Trypoxylon* (O'Neill 2001), including *T. petiolatum* (Barthélémy 2012). The rate of expansion of other solitary wasps and bees in Europe is highly-species dependent. Some species, including *Isodontia mexicana* (de Saussure, 1867), *Sceliphron curvatum* (F. Smith, 1870) and *Megachile sculpturalis* (Smith, 1853) (discovered in 1960s, 1979, 2008, respectively) have widely spread and are now common in various European countries (Bitsch 2020; Le Féon et al. 2021; Polidori et al. 2021). By contrast, other species, including *Sceliphron caementarium* (Drury, 1773), *Osmia lignaria* (Say, 1837), *Sceliphron deforme* (F. Smith, 1856), *Chalybion bengalense* (Dahlbom, 1845), *Chalybion californicum* (de Saussure, 1867), *Megachile disjunctiformis* (Cockerell, 1911) and *Pison koreense* (Radoszkowski, 1887) appear to be spreading slowly, based on the scarcity of records since their introduction (1945, 1970s, 2002, 2008, 2011, 2011 and 2017, respectively)

(Ornosa et al. 2006; Mei and Boščík 2016; Bortolotti et al. 2018; Schmid-Egger and Herb 2018; Bitsch et al. 2020; Mei and Cappellari 2021). These results demonstrate that the rate of expansion of solitary wasps and bees is difficult to predict. Future findings will be needed to establish the invasive potential of *T. petiolatum*.

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Appendix 1

Diagnosis of *Trypoxylon petiolatum* based on one male and one female specimens from Girona. See Tsuneki 1978, 1980 for descriptions of specimens from Asia.

Female. (Fig. A1)

Body length: 15.8 mm (14.7–16.5 mm). Forewing length: 8.5 mm (range: 7.8–9.0 mm).

HEAD (Fig. A2): Black. Antennae black, with the ventral surface of segments 4–12 ferruginous. Third antennal segment 0.68 mm long and 0.14 mm wide (ratio: 4.83). Head width: 2.66 mm. Interocular distance at vertex (IODv): 0.79 mm. Interocular distance at base of clypeus (IODc): 0.58 mm. Ratio IODv/IODc: 1.36. Ratio IODv/HW: 0.30. Hind ocellus diameter: 0.19 mm. Distance between inner margins of hind ocelli: 0,19 mm. Edge of clypeus rounded, with widely subtruncated apex. Frons without shield-like structure. Clypeus and most of the face covered with silvery hairs. Mandibles reddish brown in the middle, darkened at both ends. Maxillary palps: segments 1–2 and base of 3 brown, apex of 3 and 4–6 yellowish.

MESOSOMA (Fig. A3): Black. Pronotal collar flat, without tubercles. Pronotal lamina produced in an obtuse triangle. Scutum smooth and shiny, without microsculpture, only with scattered shallow punctuation (points 15–20 µm Ø, interspaces 1–4 wider than points) (Fig. A3). Parapsidal lines not depressed. Scutum covered with relatively long setae (0.11–0.26 mm) and shorter brown setae.

Propodeum without lateral carinae. Propodeum enclosure with median longitudinal furrow weakly impressed, shallow. Larger part of propodeal side smooth and shiny below, with some faint striae in the anterior part, puncticulate at the top.

Figure A1. Dorsal habitus of *Trypoxylon petiolatum* female. Scale bar: 5mm.

Figure A2. Front view of female head.

Figure A3. Dorsal view of female thorax and propodeum.

LEGS: Black. Fore and mid tibiae black, except the basal and apical ends, which are brown. Hind leg tarsi black. The basitarsi and parts of the intermediate tarsal segments of the mid and fore legs are yellowish.

METASOMA: Gaster black and red. The apex of Tergum1 (T1) is red. T2 and the basal ¾ of T3 are also red, with dorsal black stains. T1 long (longer tan T2 + T3) and slender, flask-shaped, basally with parallel sides, with an abrupt apical swelling. T1 3.94 mm long and 0.82 mm wide (ratio = 4.83). T1 is 0.28 mm wide at the subbasal level, just after the broadened part.

Male. (Fig. A4)

Body length: 12.5–13.7 mm. Forewing length: 7.5–7.7 mm.

Males are similar to females, with the following main differences:

HEAD (Fig. A5): Antennae entirely dark brown to black. Third antennal segment 0.42 mm long and 0.16 mm wide (ratio: 2.57). Last antennal segment (A13) 0.63 mm long, longer than the preceding three segments combined (A10-A12, 0.57 mm), but shorter than the preceding four segments combined (A9-A12, 0.77 mm). A13 length/width= 3.0. Head width: 2.52 mm. Interocular distance at vertex (IODv): 0.73 mm. Interocular distance at base of clypeus (IOCc): 0.58 mm. Ratio IODv/IODc: 1,26. Ratio IODv/HW: 0.29. Hind ocellus diameter: 0.17 mm. Distance between inner margins of hind ocelli: 0.14 mm.

MESOSOMA (Fig. A6): Pronotal lamina produced in an obtuse triangle.

LEGS: Fore tarsi pale brown; mid and hind tarsi black.

METASOMA (Fig. A7): Gaster black and red. The apex of T1 is red. T2, and the basal ¾ of T3 are red, with dorsal black stains. T1 3.7 mm long, longer than T2 + T3 together (1.1+1.0 = 2.1 mm); T1 slender, flask-shaped, with an abrupt apical swelling; T1 is 0.22 mm wide at subbasal level, just after the broadened part, and maximal width (subapically) is 0.65 mm. Ratio T1 length/maximal width= 5.68. The genitalia is shown in Fig. A8.

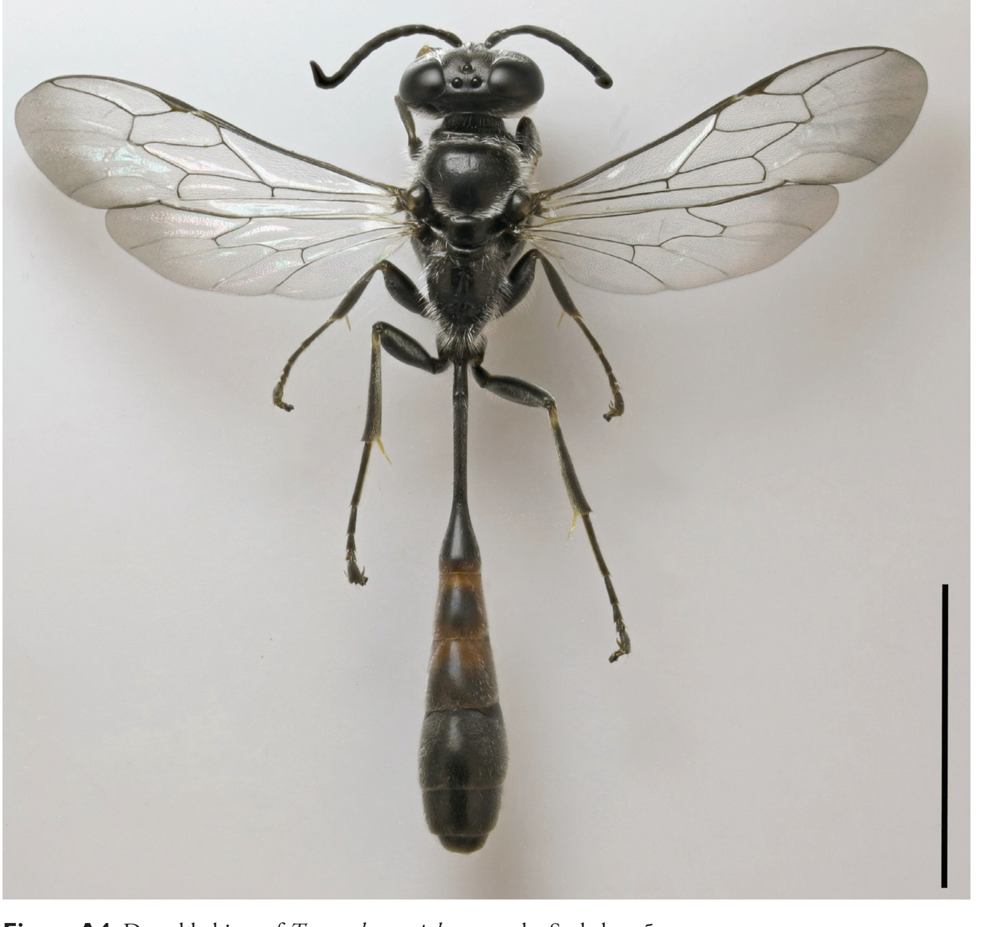

Figure A4. Dorsal habitus of *Trypoxylon petiolatum* male. Scale bar: 5 mm.

Figure A5. Front view of male head.

Figure A6. Lateral view of male head and mesosoma.

Figure A7. Lateral view of male metasoma.

Figure A8. Male genitalia, ventral view. Scale bar: 0.5 mm.