



The larval morphology and nest habits of *Trypoxylon (Trypargilum) rogenhoferi* Kohl 1884 (Insecta: Hymenoptera: Crabronidae)

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Abstract

The present study describes different preimaginal stages of *Trypoxylon rogenhoferi* examined by Scanning Electron Microscopy (SEM) and compares the results with observations on closely related species. Some notes on the nesting habits of this species, including their spider prey, nest parasites, and development time are provided. In short, *T. rogenhoferi* proved quite similar to the previous report on *T. albitarse* although SEM images are rarely presented in such descriptions. In fact the present study emphasized the importance of SEM images to describe fine morphological details that can be useful characters for taxonomic and phylogenetic studies. Images of some earlier development stages (first and second larval instar and egg) are presented for the first time, and compared with the few available data from other hymenopterans.

Resumo

O presente estudo apresenta a descrição de diversos estágios do desenvolvimento da vespa caçadora *Trypoxylon rogenhoferi* por meio de microscopia eletrônica de varredura (MEV). Os resultados obtidos são comparados com achados com outras espécies próximas. Também são fornecidas informações a cerca da biologia da espécie no local de estudo, como presas e parasitóides observados e tempo de desenvolvimento. A larva madura desta espécie se demonstrou bastante similar ao pouco que foi descrito com *T. albitarse*, apesar de que raramente imagens de MEV são apresentadas nestas descrições. O presente estudo demonstra a importância de imagens de ultraestrutura que podem revelar detalhes úteis para a diagnose de espécies e estudos filogenéticos. Pela primeira vez se descrevem estádios imaturos mais jovens de vespas deste grupo, que foram comparados com dados de outros grupos de himenópteros.

Keywords: mud-daubing wasps, spider-hunting wasp, immature stages, developmental time, taxonomy

Introduction

The genus *Trypoxylon* Latreille comprises some 651 species of spider-hunting wasps that build mud nests on vegetation, crevices, and buildings (Evans 1957; Pulowski 2012). *Trypoxylon rogenhoferi* Kohl, along with some closely related species from the subgenus *Trypargilum* Richards—*T. lactitarse* Saussure, *T. albitarse* Fabricius, *T. aurifrons* Richards and *T. nitidum* Saussure—is a common wasp in Brazil, where it can be obtained from the field by using artificial nests (Santoni *et al.* 2009).

The importance of immature morphology to insect systematics and taxonomy and the paucity of information in this field were extensively discussed in previous studies (e.g. Capek, 1970; Short 1959; Fynlayson 1967; Wheeler & Wheeler 1976; Schultz & Meyer 1995). The present study is part of a recent effort to assess the general deficiency in the morphological information about larval stages within Hymenoptera.

Unlike most genera of hymenopterans, the larvae of quite a few species of *Trypoxylon* have been described (Williams 1919, Soika 1934, Evans 1957, 1959, Iida 1969, Yoshimoto 1964, Asis *et al.* 1994, Buys 2003, 2005, 2007). These descriptions were made with various levels of detail, and some morphological characters were suggested for species diagnosis. However, morphological structures were usually illustrated with line drawings and without scanning microscopy to clarify details (with the only exception of Buys 2007). As has been demonstrated in some recent studies (e.g. Fox *et al.* 2007), scanning electron microscopy (SEM) images and larger sample sizes can drastically improve the quality and usefulness of insect larval descriptions. Also, interesting information can be obtained from analysing immature stages other than the last larval instar (see, for instance, Fox *et al.* 2006, 2012).

Materials and Methods

Immature specimens (n = 17) were obtained from 8-cm-long carton tubes placed at a grassy area in the municipality of Rio Claro, São Paulo, Brazil. Such artificial nests were placed on wooden shelves in an open field and inspected weekly for nests of *T. rogenhoferi*.

Species identification was made based on characters provided in Conville (1982), notes in Santoni (2008), and by direct comparison with specimens deposited in the Museu de Zoologia of the University of Sao Paulo (MZSP). Distinctive features observed include cocoon form, inflated hindfemora, and general clypeus shape (Conville 1982), males' clypeus presenting a pronounced thorn-like upright 'nose' (Sartoni 2008).

Nest tubes containing the specimens were brought to the laboratory, carefully opened, and their contents preserved in 80% ethanol. Eggs and larvae were transferred into empty transparent plastic Bic® pens, where they were reared using spiders as prey. The development rates could thus be recorded regularly. Room conditions varied within 23–28°C and 50–70% of relative humidity.

Specimen preparation for SEM observations and image recording followed standard procedures, as detailed in Solis *et al.* (2010). Some specimens were prepared for observation under a compound microscope (Zeiss MC80) following procedures described in Evans & Lin (1956). In brief, these specimens were heated in potassium hydroxide 10% for 15 minutes, their heads and parts of the body tegument were excised and mounted on glass slides with a drop of glycerine. Digital pictures were taken with a SONY camera directly from the eyepiece. Terminology employed follows Evans & Lin (1956). Three eggs, one first instar-larva, three second-instar larvae, and several mature larvae were observed.

Voucher specimens are deposited in the entomological collection of MZSP and in the Collection of Arachnida and Myriapoda of the Instituto Butantan (Sao Paulo, Brazil).

Results

Morphological description

Egg

Typically hymenopteriform, elongate and slightly curved, measuring 1.5 mm (n = 3); yellowish white; without outer orifices or ornamentation (Fig. 1). Quite fragile in comparison with eggs of other species previously studied by the authors (*i.e.*, *Ampulex compressa* Jurine in Fox *et al.* 2006; *Evania appendigaster* L. in Bressan-Nascimento *et al.* 2008; and unpublished results of EGPF with *Tetrapedia diversipes* Klug and *Tetrasticus hagenowii* Ratzeburg).

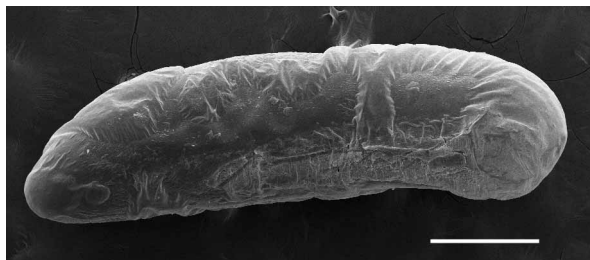


FIGURE 1. Scanning electron micrograph of *Trypoxylon rogenhoferi* egg. Scale bar: 400 µm.

First instar larva (Fig. 2)

White, about 1.4 mm long, not active, remaining attached to the paralyzed spider's abdomen, while slowly consuming its body and juices. Head capsule notably large, being about one third of total body length, slightly curved (not shown); surface smooth (Fig. 2A). Mandibles robust and triangular, pointed at apex (Fig. 2B). Spiracle peritreme rounded and unarmed, about 6 μm in diameter (Fig. 2C). Body integument spinulose (Fig. 2D; 2E).

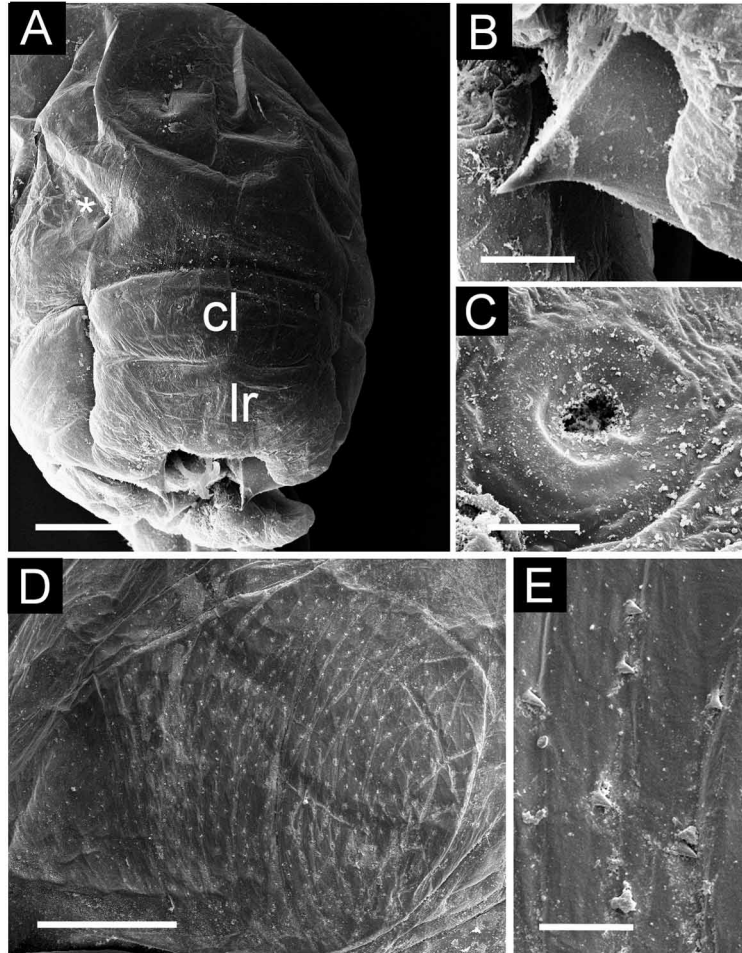


FIGURE 2. Morphological aspects of the first instar larva of *Trypoxylon rogenhoferi*. A—Head capsule; B—Right mandible; C—Thoracic spiracle; D—Body integument surface; E—detail on spinules of body surface. Asterisk = tentorial pit; cl = clypeus; lr = labrum. Scale bars (μm): 200; 40; 20; 300; 25.

Second instar larva (Fig. 3)

Body. Length 3.2 mm long \times 1.7 mm wide ($n = 3$); straight and plump (not shown). Apparently nine pairs of unarmed, round, hard-to-spot spiracles (not shown). Body integument spinulose, no setae. Head capsule 1.1 mm wide \times 0.9 mm high ($n = 2$) (Fig. 3A), with 12 ten- μm -long setae on each gena (Fig. 3B), punctures absent; tentorial pits well-defined (Fig. 3A), clypeus about 450 μm wide and clearly detached from cranium, with six six- μm -long setae (Fig. 3A; Fig. 3D).

Mouthparts. Labrum quadrangular, 0.46 mm wide, with about 18 eight- μm -long setae and ten basiconic sensilla (Fig. 3D). Maxillary palps 50 μm long, with five sensilla—three basiconic and two setaceous; galeae 15 μm high and topped with two setaceous sensilla (not shown). Mandibles robust and sclerotized, triangular with many serial teeth (Fig. 3D). Labial palps with five sensilla, two basiconic and three setaceous; spinneret a 40- μm -long horizontal slit (Fig. 3C; 3D); few spinules near mouth entrance.

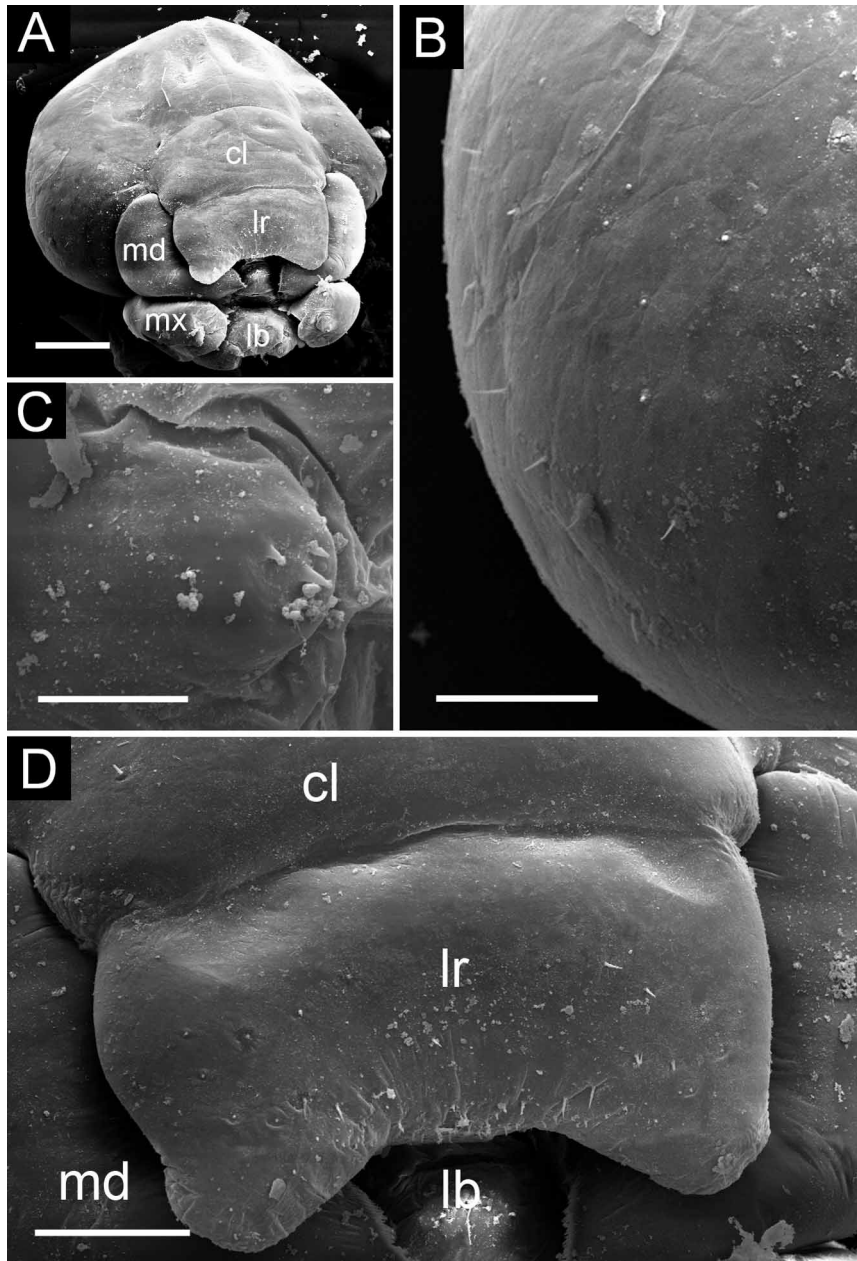


FIGURE 3. Morphological aspects of the intermediary (probably second) instar larva of *Trypoxylon rogenhoferi*. A—Head capsule; B—Genal area; C—Labial palpus; D—Labrum and mandibles. Cl = clypeus, lr = labrum, mx = maxilla, md = mandible, lb = labium Scale bars (μm): 210, 100, 20, 100.

Mature Larva (Figs. 4 and 5)

Body. Yellowish white, with shades of brown, some specimens turning darker, possibly as a result of impregnation with fixative; about 1.4 cm long and 3.3 mm wide ($n = 3$) (Fig. 4A). Body segmentation clearly marked, without dorsal annulets yet with well developed pleural lobes (Figure 4A). Body integument mostly smooth, with spinules on pleural lobes (now shown). Spiracle peritremes unornamented, but surrounded by ten equally-sized, circular ridges on each side (Fig. 4C); unpigmented and inconspicuous in fresh specimens (not shown).

Head capsule. Greatly elliptical, lightly sclerotized and mostly pigmented around tentorial pits; measuring 1.35–1.4 mm at maximum width and 1.1–1.2 mm ($n = 4$) from distal border of clypeus to the occipital border (Fig. 4B). Parietal bands feebly pigmented 0.5 mm-long ($n = 2$), completely disappearing after treatment with KOH 10%, metopic suture absent; antennal orbits lightly delimited and widely separated (Fig. 4B), about 50 μm in diameter, mostly with three basiconic sensilla, but some with two or even four (number of sensilla not always symmetrical; inset of Fig. 4B shows one specimen with two sensilla). Surface of head capsule mostly smooth, but

with eight setae on the frons and one seta near the occipital border on each side, and 11–13 setae on each gena (not shown). Tentorial pits slit-like and pronounced just over the proximal border of clypeus (not shown). Clypeus 0.80 mm wide \times 0.22 mm high, with eight setae and 10–15 punctures on the dorsal surface near the division with the labrum (not shown).

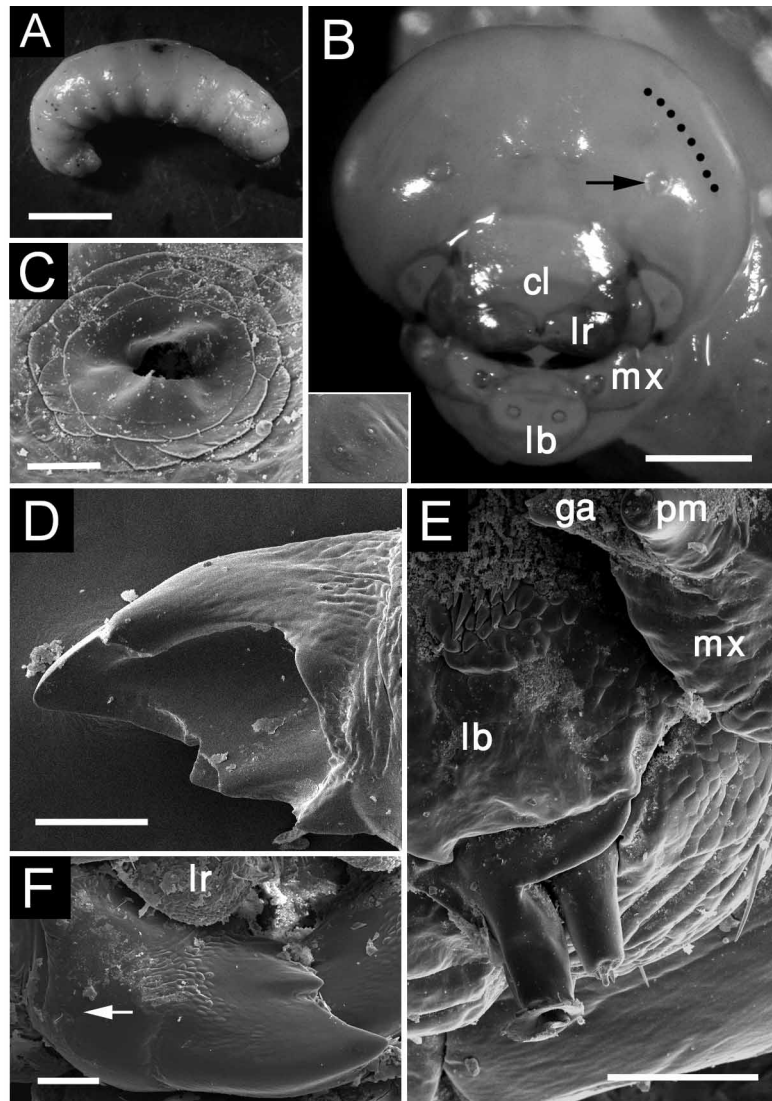


FIGURE 4. Morphological aspects of the mature larva of *Trypoxylon rogenhoferi*. A—Body on side view. B—Head capsule in full frontal view; inset: antennal orbit; C—Thoracic spiracle; D—Mandible in inner side view; E—Maxilla and labial palp; F—Mandible in frontal view. Cl = clypeus, lr = labrum, mx = maxilla, lb = labium, pp = pseudopalpus (sericteries), pm - maxillary palpus, pl = labial palpus, ga = galea, black arrow = antennal orbit, black dots = parietal band, white arrow = seta on mandible base. Scale bars (μ m): 400, 200, 20, 100, 70, 100.

Mouthparts. All mouthparts distinctly sclerotized at base. Labrum somewhat bilobed (Fig. 4B, 5A), 0.6 mm wide and 0.3 mm high, with 20–25 setae on its lower part, mainly concentrated on the medial groove; anterior surface markedly papillose on the lower portion, especially on the lobes (Fig. 5A). Posterior surface of labrum (ephypharynx) densely covered with spine-like papillae, except for the lateral borders; two groups of four setaceous sensilla on the medial portion (Fig. 5B; 5C). Maxilla fleshy and lobose, with six setae and one setaceous sensilla, spinulose at inner portion and lacinia; maxillary palps finger-like, about 44 μ m high, with five basiconic sensilla of variable shapes; galea finger-like and 28 μ m high with two basiconic sensilla. Mandibles massive and gauntlet-shaped, with four prominent teeth; mandible surface with flattened papillae on its anterior surface and one seta near the base (Fig. 4D; 4F). Labium relatively small, and roughly ovoid, with three setae on each side of its ventral surface; opening of sericteries with two finger-like, 90 μ m high, tulip-shaped processes (termed pseudopalps, see Fig. 4F); labial palps also finger-like (Fig. 4F), about 65 μ m high and culminating in five basiconic sensilla.

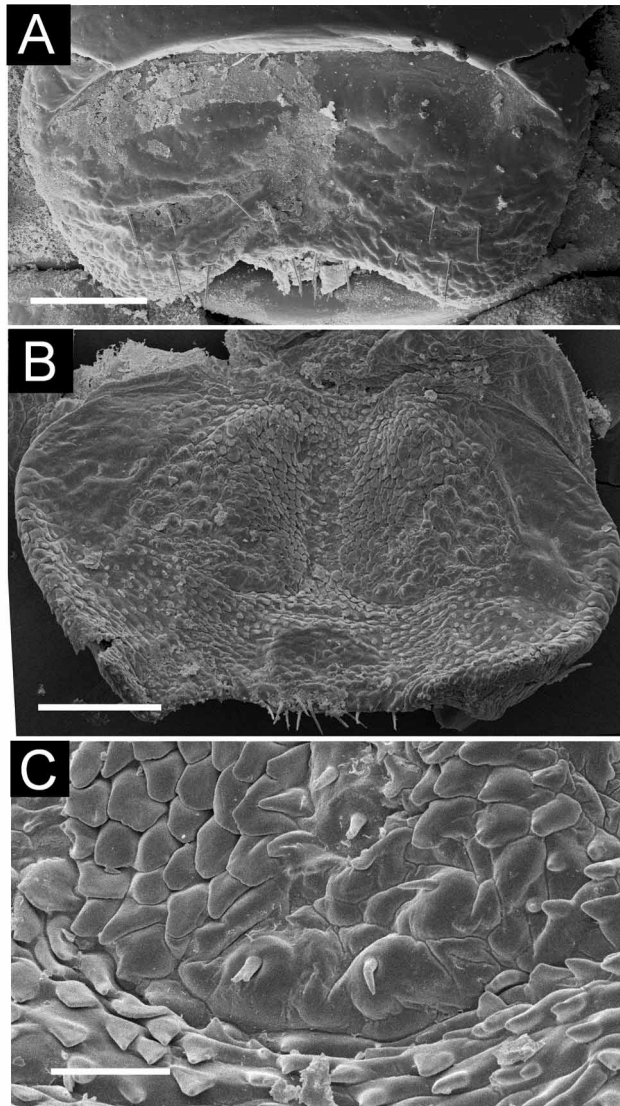


FIGURE 5. Surface aspects of labrum of *Trypoxylon rogenhoferi*, A—anterior surface of labrum; B—epypharynx ; C—closer view on sensory area of epypharynx. Scale bars (μm): 100, 100, 20.

Pupa (Fig. 6)

Prepupa clearly distinguishable from mature larva as it is less active, and acquires a distinct shape from the appearance of a constriction between the developing tagma (Fig. 6A); oxalate impregnations abundant. Pupae exarate, yellowish white when young and getting darker with a strong orange hue while maturing into imagoes; length 1.60–1.72 cm ($n = 3$) (Fig. 6B). Cocoons dark brown and smooth, elongate and fragile, except for the thicker round anterior cap (Fig. 6C).

Notes on nesting habits

Carton trap nests used by *Trypoxylon* can be easily recognized in the field as the wasps close the nest entrance with a thin clay cap (clay tonality varied from gray to reddish brown). Upon unrolling the paper nest tube, two to five five-cm-long cells were found inside the carton nests ($n = 17$), each separated from the next by a thin layer of clay. Each cell contained either live paralyzed spiders along with one wasp egg or larva, or a fully grown larva or cocoon. Only one egg was found per spider/cell, always found attached by one end to the abdomen of the paralyzed spider placed near the proximal end of nest cells. The number of spiders provisioned within each cell varied from seven to 18, apparently depending on the size of the captured spiders. The spiders were clearly alive, yet practically

unable to move. All spider species captured were from the family Araneidae; they included *Ocrepeira* sp., *Alpaida leucogramma* (White), *Alpaida* sp., *Alpaida bicornuta* (Taczanowski), and *Parawixia bistrata* (Rengger). The latter species comprised about 70% of the captured prey, and were always immature; other specimens were always mature, mostly females. Usually all spiders were entirely consumed by the larvae, so that few vestiges remained outside the fully-formed wasp cocoon.

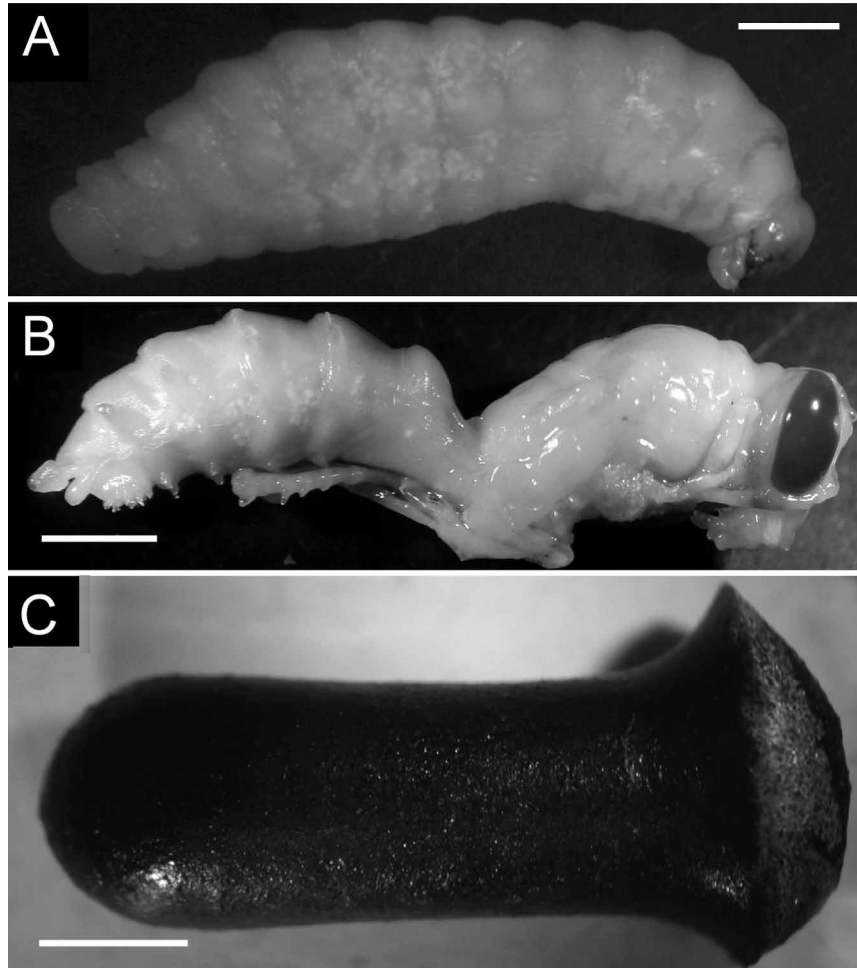


FIGURE 6. Post-larval development stages of *Trypoxylon rogenhoferi*, A—Prepupa; B—Pupa; C—Cocoon. Scale bars (μm): 250, 250, 400.

Eggs took about 72 h to hatch ($n = 7$), and complete development from egg to cocoon varied from 31 to 40 days ($n = 4$). Following molts proved impracticable, as each larval skin was cast off very slowly and was exceedingly delicate, their remains accumulating as a delicate pack around the terminal end of the larval body. We suspect the larvae (always quite active and eating during observations) consumed their cast head capsules, as no vestiges remained. Based on personal impressions of growth rates, we would estimate this species has three or four larval instars, but this would have to be confirmed by other methods (e.g., Dyar's rule) based on a greater sample size. It is worth noting that larvae were very fragile and sticky, making them difficult to manipulate as they were easily killed when handled. These characteristics make precise instar determination complicated in this species.

Species parasitizing the nest tubes

Out of 21 inspected nest cells, five were parasitized by *Mellitobia* cf. *hawaiensis* Ferriere (Hymenoptera, Eulophidae) and four were parasitized by *Anthrax o. oedipus* Fabricius (Diptera, Bombyliidae) (identification based on Marston 1971).

Discussion

Larval description

Our observations confirmed some characteristics of larvae of some other *Trypoxylon*, such as i) maxilla apically papillose; ii) maxillary palpi slightly longer than galeae, and iii) head capsule roughened at borders (the “cephalic rugosities” mentioned in Buys 2007). The following set of characteristics was common to all larvae in the subgenus *Trypargilum* hitherto described (listed in Table 1): i) punctures on genae and clypeus; ii) a basal seta on mandible; iii) spinulose epypharynx. *Trypoxylon rogenhoferi* differed from other species mainly in having limited spinules on the epypharynx and for peritreme ornamentation (see differences in Table 1). In fact, the larva of *T. rogenhoferi* is strikingly similar to *T. tridentatum*, differing in the spiracle peritreme with ridges, and in the fact that all spiracle peritremes were of about the same size (Evans 1957).

Evans (1957) employed mainly the shape of labrum as a character for differentiating between some species of *Trypargilum*; however we did not find it a good character as the differences in the shape of the “apical margin” of labrum were not quite obvious from the illustrations given by the author, and labrum shape in our observations seemed to be dependent on position of the analyzed specimen (for example, compare Fig. 5A and 5B of the same specimen, in the first the labrum seems clearly bilobed while in the second the labrum appears quadrangular).

The outer ornamentation of the peritreme opening, illustrated in Fig. 4C, is clearly the result of the unique bulbous nature of the subatrium originally observed by Evans (1957) in *Trypargilum tridentatum* Packard and *Trypoxylon nitidum* Smith upon direct dissection of spiracles. For the first time in larvae of solitary wasps, the present description recorded variation in the number of antennal sensilla, even between the antennae of the same specimen. Similar phenomena seem to be frequent among ant larvae (Solis *et al.* 2010, Fox *et al.* 2012), and was only observed upon analyzing numerous larvae. This illustrates how larger sample sizes can prevent intraspecific exceptions to be taken as reliable diagnostic specific characters.

Integument structure (e.g. presence or absence of setae and spinules) cannot be trusted as morphological characters for species diagnosis at our present state of knowledge, as these structures were frequently overlooked in previous descriptions. The larval descriptions of Evans lacked ultramorphological details and some important aspects were often overlooked (as can be seen from Table 1), including details of body integument. Some of these characters would have to be revisited in the described species if they are to be used as taxonomic characters.

The species of *Trypoxylon* are frequently difficult to identify. The Wheelers had the impression, in their long series of descriptions of ant larvae (for a general idea, refer to Wheeler & Wheeler 1976), that different larva species within the same genus were quite often exceedingly similar. Thus, larval characters are not very reliable at the species level, but are better for use in assessing phylogenetic relationships at the genus level. In fact, some similar congeneric species of ants have identical larvae (see, e.g., Fox *et al.* 2012; Solis *et al.* 2013). Yet, combining our findings with those of previous descriptions shows the existence of useful characters for species-level identification in *Trypoxylon* wasps (Table 1). It is thus possible that this tendency is widespread in larvae of apoid wasps, in contrast with larvae of ants.

The only previous description of younger stages of a solitary wasp was that of Fox *et al.* (2006), wherein details on the egg, first and second instar of *A. compressa* were provided. The first instar larva of *A. compressa* was twice as large, yet had some characteristics in common with the first instar larva of *T. rogenhoferi*: spinulose integument and reduced mouthparts. However, the newly-hatched larva of *A. compressa* had mandibles with three apical teeth (Fox *et al.* 2006), possibly for fixation on its cockroach host. The newly hatched larva of *T. rogenhoferi* (Fig. 2B) had very simple mandibles without any subapical teeth, somewhat similar to those of first-instar larvae of ants (e.g. Fox *et al.* 2007), probably specialized for tearing the soft tissues of the paralyzed spiders.

Nesting habits

Spiders captured by *T. rogenhoferi* in this study are consistent with most records given for the same species by Santoni *et al.* 2009, at least at the genus level, as the authors did not give the species of all their records. However, a fundamental difference in the present observations is the occurrence of immatures of the social spider *P. bistrriata*, which were in fact the most frequently captured prey. *Trypoxylon lactitarse* was previously reported to capture *Parawixia audax* Blackwall by Buschini *et al.* (2008) and Camillo and Brescovit (1999). This is thus the first time *P. bistrriata* is recorded as prey of *Trypoxylon*, and its immature forms were the preferred by the wasps within the studied area. It should be noted that the immature forms are easier for the wasps to carry and insert into the nests because of their small size (females measuring 6–9 mm), while adult females reach over 16 mm (Levi, 1992). We believe that somehow *P. bistrriata* was more available or conspicuous to the wasps in the present study period and area, possibly as a result of local population dynamics.

TABLE 1. Morphological characters of described mature larvae of mud-daubing wasps of the genus *Trypoxylon*.

	<i>Trypoxylon albitarse</i>	<i>Trypoxylon clavatum</i>	<i>Trypoxylon johannis</i>	<i>Trypoxylon arizonense</i> (= <i>californicum</i>)	<i>Trypoxylon spinosum</i>	<i>Trypoxylon rubrocinctum</i> + <i>tridentatum</i> (= <i>tridentatum</i>)	<i>Trypoxylon striatum</i> + <i>politum</i> (= <i>lactitarse</i>)	<i>Trypoxylon rogenhoferi</i>
Body dimensions (mm)	17.0 × 5.0	13.0 × 4.0	15.0 × 4.0	9.0 × 3.0	13.0 × 3.6	13–15.0 × 3.5–4.0	20.0 × 5.5–6.0	14.0 × 3.5
Body integument	spinulose and setose (2 ≠ sizes)	no spinules, few setae	?	few setae, no spinules	?	few setae	few setae	few setae, spinulose
Spiracle peritreme ornamentation	unarmed	unarmed	unarmed	unarmed	?	unarmed	unarmed	Unarmed
Head capsule size (mm) and ornamentation	1.7 × 1.8, few setae	1.16 × 1.00	1.40 × 1.25	1.20 × 1.12, setose	1.28 × 1.10	1.2 × 1.1	1.5–2.0 × 1.30–1.75	1.4 × 1.2
Presence of punctures on head capsule	Punctures on clypeus and genal areas	Setose, punctures on gena and clypeus	?	Punctures on genal areas	?	?	?	Punctures on clypeus
Approximate number of labral setae	30	?	20	11	22	24	32	22–25
Epypharynx sculpture	spinulose	spinulose	spinulose	weakly spinulose, naked at sides	?	weakly spinulose	spinulose	Weakly spinulose
Basal seta on the base of mandible	Yes	?	?	Yes	Yes	?	?	Yes

Note: Information retrieved from published literature, Williams 1919, Soika 1934, Evans 1957, 1959, Iida 1969, Yoshimoto 1964, Asis et al. 1994, Buys, 2003, 2005, 2007

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