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# The first species of *Prococcophagus* Silvestri (Hymenoptera: Aphelinidae) from America north of Mexico

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# The first species of *Prococcophagus* Silvestri (Hymenoptera: Aphelinidae) from America north of Mexico

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**Abstract.** *Prococcophagus tobiasi* (Myartseva) (Hymenoptera: Aphelinidae) is newly recorded from the state of Florida. This represents the first record of the genus *Prococcophagus* Silvestri in the United States. Amendments are made to the original description based on the newly collected specimens, and the species is placed in the context of the genus based on a phylogenetic analysis of 28S rDNA. The status of the specimens comprising the type series is discussed and notes are made on the unusual coloration exhibited by living specimens.

**Key words.** Coccophaginae, coloration, parasitoid, phylogenetic analysis, Prococcophagini.

**ZooBank registration.** urn:lsid:zoobank.org:pub:99423081-F21A-4B9C-94AF-CAB2BBFC5EA4

## Introduction

Ongoing phylogenomic analyses of Chalcidoidea (Hymenoptera: Proctotrupomorpha) have resulted in the resurrection of taxa previously synonymized based solely on morphology (Burks et al. 2022; Kresslein et al. 2025). The aphelinid genus *Prococcophagus* Silvestri (Coccophaginae: Prococcophagini) is one such example (Silvestri 1915). Originally described for a single female collected in Eritrea, *Prococcophagus* was synonymized with *Coccophagus* Westwood by Shafee et al. (1985) and Viggiani (1985), following an idea originally put forth by Hayat (1983). The same year that *Prococcophagus* was established, Girault (1915) erected *Taneostigmoidella* Girault for three species collected in Queensland, Australia. He then synonymized his own genus with *Prococcophagus* two years later (Girault 1917). Silvestri (1915) separated *Prococcophagus* from *Coccophagus* based on the flattened antennal scape of the adult female and the proximity of the toruli to the clypeal margin. Hayat (1983) deemed these characters "weak", further stating that the genus may ultimately become a species-group of *Coccophagus*. Following its synonymy, Hayat (1988) erected the *Coccophagus varius* species-group for the then 11 species previously described in either *Prococcophagus*, *Taneostigmoidella*, or *Aneristus* Howard (also a synonym of *Coccophagus*). An additional 15 species (mostly from China) have since been described in the *varius* group (Hayat and Zeya 1993; Huang 1994; Hayat 1998; Myartseva 2004; Wang et al. 2020; Qin et al. 2022). Recently, Kresslein et al. (2025) reinstated *Prococcophagus* as a valid genus and established the tribe Prococcophagini based on the results of published (Cruaud et al. 2024) and unpublished phylogenomic analyses (R.L. Kresslein, unpublished data).

The hosts of *Prococcophagus* include soft scales (Coccidae) and pit scales (Asterolecaniidae), two taxa of considerable economic importance. For this reason, two species [*P. probus* Annecke and Mynhardt and *P. eusaissetiae* (Özdikmen) (the latter as P. *saissetiae* Annecke and Mynhardt)] were introduced from South Africa into olive orchards in central California (USA) in 1978 to help control the highly polyphagous and cosmopolitan black scale, *Saissetia oleae* (Olivier) (Daane et al. 1991). *Prococcophagus probus* was established, albeit at low densities, which speaks to the ability of this species, and potentially other members of the genus, to acclimate outside its native range – a hallmark of a good biocontrol agent.

*Prococcophagus* is globally distributed, with most species having been described from the Old World (particularly the Afrotropical, Indomalayan, and Australasian realms) (Table 1). Only a few species have been described from elsewhere (Palearctic: Japan; Nearctic: Mexico; Neotropical: Haiti, Mexico) (Dozier 1932; Ishihara 1977; Myartseva 2004); curiously, members of the genus not imported for biological control purposes have not been known from the United States, until now. The purpose of this contribution is to (1) report the discovery of *P. tobiasi* from Florida (USA); (2) place the species within the context of the genus using molecular sequence data (28S rDNA); (3) provide amendments to the species concept of *P. tobiasi* based on morphological variation observed in the specimens relative to the original description; and (4) provide notes on the status of specimens comprising the type series, the monophyly of the genus, and the remarkable coloration of the live wasps.

# Materials and Methods

**Specimen collection.** The specimens on which this study is based were collected by sweeping vegetation using a sweep net with a triangular frame (Noyes 1982). Specimens were stored in 96% ethanol and held at -25°C until DNA extraction. One of the three specimens was not extracted, but chemically dried with hexamethyldisilazane (Heraty and Hawks 1998). This specimen was used to make notes on the coloration of the species relative to the original description.

**DNA extraction, PCR analyses, and slide mounting.** Genomic DNA was extracted from single wasps following the protocol outlined in Lahey et al. (2022) and Polaszek et al. (2013), except that 15 µl proteinase K was used per specimen. The exoskeleton of each specimen was then slide-mounted in Canada balsam following the procedure in Noyes (1982), with modification by Polaszek et al. (2013). DNA extracts were then stored at −25°C until used in PCR analyses. Two genomic regions were targeted for amplification by PCR: the standard 5′ barcode region of the cytochrome c oxidase subunit I (COI) gene (Folmer et al. 1994; Fusu and Polaszek 2017) and the 28S D2 and D3 domains of the 28S large ribosomal subunit (28S-D2-3) (Table 2). Thermocycling conditions for COI and the 28S-D2-3 region followed Andreason et al. (2019). PCR amplicons were electrophoresed in a 1.5% agarose gel stained with SYBR® Safe DNA Gel Stain (Invitrogen, Carlsbad, CA, USA) in 1X TAE buffer, and TrackIT™ 1 Kb Plus DNA Ladder (Invitrogen, Waltham, MA, USA) was used to estimate product sizes. Both strands of each amplicon were sequenced on an ABI 3730xl DNA Analyzer by Eton Bioscience, Inc. (Research Triangle Park, NC, USA). Forward and reverse sequences of each amplicon were assembled with the Geneious assembler at the Highest Sensitivity/Slow setting in Geneious Prime (version 2023.1.1). The sequences associated with this study have been deposited in GenBank under accession numbers OR835219 (28S-D2-3) and OR837746 (COI).

**Phylogenetic analyses.** A maximum likelihood phylogeny was estimated for the 28S-D2-3 region of six *Prococcophagus* and 16 *Coccophagus* species using IQ-TREE (v.2.1.3) (Hoang et al. 2018; Kalyaanamoorthy et al. 2017; Katoh et al. 2013; Minh et al. 2020). These analyses followed the protocol of Lahey et al. (2022). The taxa selected for comparison with *P. tobiasi* correspond to the same GenBank accessions as those used by Qin et al. (2022), except for *C. bivittatus* Compere, which was removed because its sequence was identical with, and shorter than, that of *C. longifasciatus* Howard. Two species of *Coccobius* Ratzeburg and *Diaspiniphagus fuscipennis* (Girault) were used as outgroups.

**Morphology.** Terminology of morphological structures follows Compere (1936) and Gibson (1997).

**Imaging.** Slide-mounted specimens were imaged with a Keyence BZ-X810. Composite images were imported into Adobe Photoshop 2024 to correct for brightness and contrast before compilation of the figure plates.

**Collections.** The two slide-mounted specimens (OSUC 864110 and 864111) are deposited in the Smithsonian National Museum of Natural History (USNM), Washington, DC, USA. The card-mounted specimen is deposited in the Florida State Collection of Arthropods (FSCA), Gainesville, FL, USA.

**Table 1.** *Prococcophagus* Silvestri species, type localities, and scale and plant host information.

| ***Prococcophagus* species** | **Type locality** | **Scale host** | **Plant host** |
|---|---|---|---|
| *albifuniculatus* Huang | China: Fujian | | |
| *anchoroides* Huang | China: Fujian | | |
| *argentiscutellum* (Girault) | Australia: Queensland | | |
| *asterolecanii* (Dozier) | Haiti: Morne à Cabrits | *Asterolecanium aureum* | *Annona* sp. |
| *aurantifrons* Compere | Australia: New South Wales | *Inglisia* sp. | |
| *breviclavulus* (Chen and Li) | Chinga: Yunnan | | |
| *caudatus* Huang | China: Fujian | | |
| *dilatatus* Huang | China: Fujian | | |
| *equifuniculatus* Huang | China: Fujian | *Saissetia chimanimanae* | |
| *eusaissetiae* (Özdikmen) | South Africa: Swartruggens | *Saissetia oleae* | |
| *fumadus* (Hayat) | India: Orissa | | |
| *hispaniolae* (Dozier) | Haiti | *Ceroplastes giganteus* | *Ficus rubricosta* |
| *lii* Huang | China: Fujian | | |
| *mixtus* (Girault) | Australia: Queensland | | |
| *narendrani* (Hayat and Zeya) | India: Kerala | | |
| *neserorum* Annecke and Mynhardt | South Africa: Tulbagh | *Pulvinariella mesembryanthemi* | *Carpobrotus* sp. |
| *nipponicus* Ishihara | Japan: Matsuyama | *Pulvinaria floccifera* | *Ilex integra* |
| *nympha* (Girault) | Australia: Queensland | | |
| *pellucidus* Huang | China: Fujian | | |
| *perlucidus* (Chen and Li) | China: Yunnan | | |
| *probus* Annecke and Mynhardt | South Africa: Genadendal | *Saissetia oleae* | *Leucodendron salignum* |
| *srilankensis* (Hayat) | Sri Lanka: Punduloya | *Bambuaspis delicatum* | |
| *tobiasi* (Myartseva) | Mexico: Morelos | | |
| *varius* Silvestri | Eritrea: Keren | *Parasaissetia nigra* | *Maytenus senegalensis* |
| | | *Saissetia jocunda* | *Celtis africana* |
| | | *Saissetia oleae* | *Nerium oleander* |
| *yunnana* (Wang, Huang and Polaszek) | China: Yunnan | Coccidae | *Kopsia fruticosa* |
| *zeyai* (Hayat) | India: Tamil Nadu | Coccidae | |

**Table 2.** PCR primer sets used in this study.

| Primer | Orientation | Region | Sequence (5′–3′) | Reference |
|---|---|---|---|---|
| MChaF1 | Forward | COI | CCTCGAATAAATAATATAAGATT | Fusu and Polaszek 2017 |
| HCO2198 | Reverse | | TAAACTTCAGGGTGACCAAAAAATCA | Folmer et al. 1994 |
| D23F | Forward | 28S-D2-3 | GAGAGTTCAAGAGTACGTG | Park and O'Foighil 2000 |
| D3B | Reverse | | TCGGAAGGAACCAGCTACTA | Nunn et al. 1996; Whiting et al. 1997 |

# Results

## Taxonomy

### *Prococcophagus tobiasi* (Myartseva)

https://zoobank.org/NomenclaturalActs/a7f763c3-9077-49ec-bece-883a1bd19b8f

Figures 1–2

*Coccophagus tobiasi* Myartseva 2004: 188–189 (original description, diagnosis, figured); Myartseva 2006: 114 (keyed); Qin et al. 2022: 123 (keyed).

**Diagnosis.** The following combination of characters separates the female of *P. tobiasi* from those of its congeners: pedicel brown ventrally, white dorsally (Fig. 1B); antenna with all flagellomeres dark brown (Fig. 1B); F1 without multiporous plate sensilla (Fig. 1B); fore wing without preapical hyaline band (Fig. 1A); axilla with 3 or 4 setae (Fig. 2C).

**Amendments to original description.** The following characters (in the format character: character state) are supplementary to the original description of the species by Myartseva (2004). The original character states coded by Myartseva (2004) are included in brackets. Color of mesoscutum: orange [yellow with orange tinge]. Color of mesoscutellum: orange [yellow with orange tinge]. Color of mesoscutal side lobe: light orange. Color of axilla: light orange [yellow with orange tinge]. Color of prosternum: fuscous. Color of mesotrochantinal plate: fuscous. Color of hind tibia: white with two faint fuscous bands [whitish]. Color of third valvula of ovipositor: dark brown [brownish]. Length of F1: ventral surface longer than dorsal surface. Number of MPS on F2: 3 [2]. Number of setae on axilla: 3 [4]. Number of setae lateral to propodeal spiracle: 4 [7; 8].

**Distribution.** Mexico; Florida (USA).

**Host.** Unknown.

**Material examined.** 1 female: USA: Florida, Thonotosassa, Trout Creek Park, 28°3′5″ N, 82°20′52″ W, Grassland, 7.VI.2015, swept, Z. Lahey, DNA Z385 (OSUC 864110); 2 females: USA: Florida, Seminole, Boca Ciega Millenium Park, 27°50.5N 82°48.5W, 23.V.2015, swept, Z. Lahey, DNA Z386, OSUC 864111 (slide mount) and FSCA 00034285 (card mount; no DNA).

**Phylogenetic analysis.** The alignment of the 28S-D2-3 region was 1,051 characters long (base pairs plus gaps). ModelFinder identified the best-fit model of nucleotide substitution according to the BIC as SYM+G4. *Prococcophagus tobiasi* was recovered as the sister taxon to *P. breviclavulus* (Chen and Li) with moderate ultrafast bootstrap support (UFBS = 79; Fig. 3). The genus *Prococcophagus* was rendered paraphyletic by *C. longifasciatus*, which was recovered as sister to *P. anchoroides* Huang. A separate analysis with two unpublished *Prococcophagus* 28S sequences also resulted in the paraphyly of the genus by *C. longifasciatus*.

**Comments.** Variation in some of the morphological characters observed in our specimens versus those listed in the original description potentially indicate that the Florida specimens are a new species. However, we opted against describing the species as new because we have limited material at hand (3 female specimens) and the types were not available for loan. Myartseva (2004) described *P. tobiasi* (as *C. tobiasi*) from a series of seven specimens, all of which remain in the Entomology Museum of the Autonomous University of Tamaulipas (UAT; Ciudad Victoria, Mexico) despite what is written in the manuscript. The holotype female, at least, is an unreturned loan

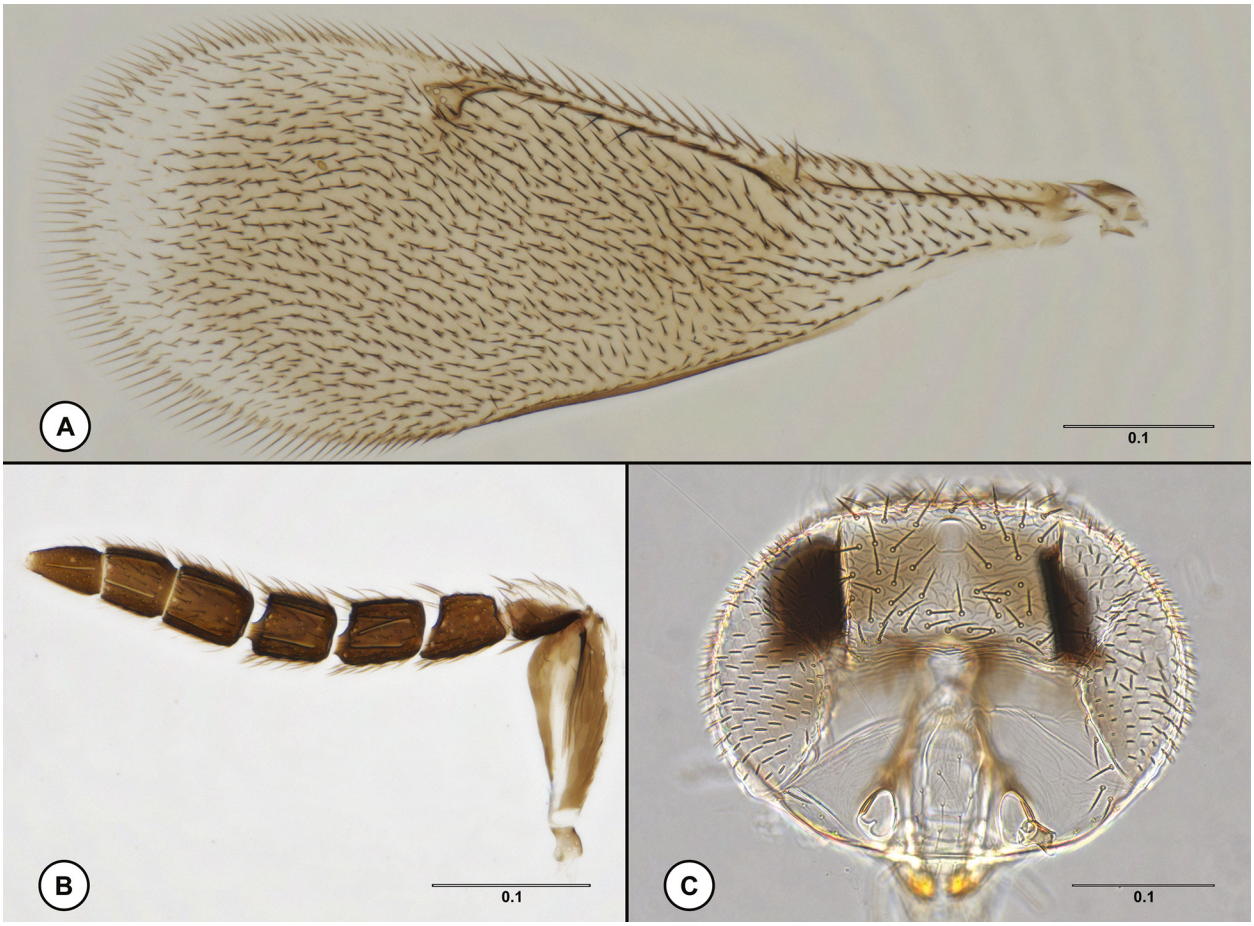


**Figure 1.** *Prococcophagus tobiasi* (Myartseva), female. **A)** Fore wing, dorsal view (OSUC 864111). **B)** Antenna, lateral view (OSUC 864110). **C)** Head, anterior view (OSUC 864110). Scale bars in millimeters.

that belongs to the UCRC (University of California, Riverside, Entomology Research Museum) (S. Triapitsyn, personal communication), and it is likely that the other specimens in the type series were also loaned from UCRC because a UCR accession number is mentioned for each of the specimens examined (e.g., UCR No. 54602). Currently, the only way to examine these specimens is by visiting UAT.

*Prococcophagus* was recently resurrected by Kresslein et al. (2025) based on the results of phylogenomic analyses (Cruaud et al. 2024; R.L. Kresslein, unpublished data), in addition to two morphological characters (pronotum medially membranous and a quadrate axilla), that place the genus outside of the tribe Coccophagini Westwood. The results of our phylogenetic analysis of 28S rDNA indicate that the genus is paraphyletic with the inclusion of *C. longifasciatus*, but an analysis with more thorough taxon sampling and additional gene regions would be needed to conclusively confirm. *Coccophagus longifasciatus* belongs to a species group of *Coccophagus* that shares several morphological similarities with *Prococcophagus*, including the excentric articulations of the funiculars that result in some antennomeres being longer ventrally than dorsally, flagellomeres with few MPS, medially membranous pronotum, thorax relatively flat, propodeum with slight to prominent medial projection, and fore wing with a 'swollen' stigmal vein (Hayat 1992). Female members of *Prococcophagus* are morphologically distinct from *C. longifasciatus*, and other members of the *ochraceus* group, by the distinct infuscation of the fore wing, flattened antennal scape (in most species), and contrasting coloration of at least some antennomeres (Kresslein et al. 2025). If any action were to be taken, it would be to expand the concept of *Prococcophagus* to include members of the *ochraceus* group. It would be ill-advised, however, to make such a decision based on the analysis of a single gene without first increasing the taxon sampling to include members of all currently

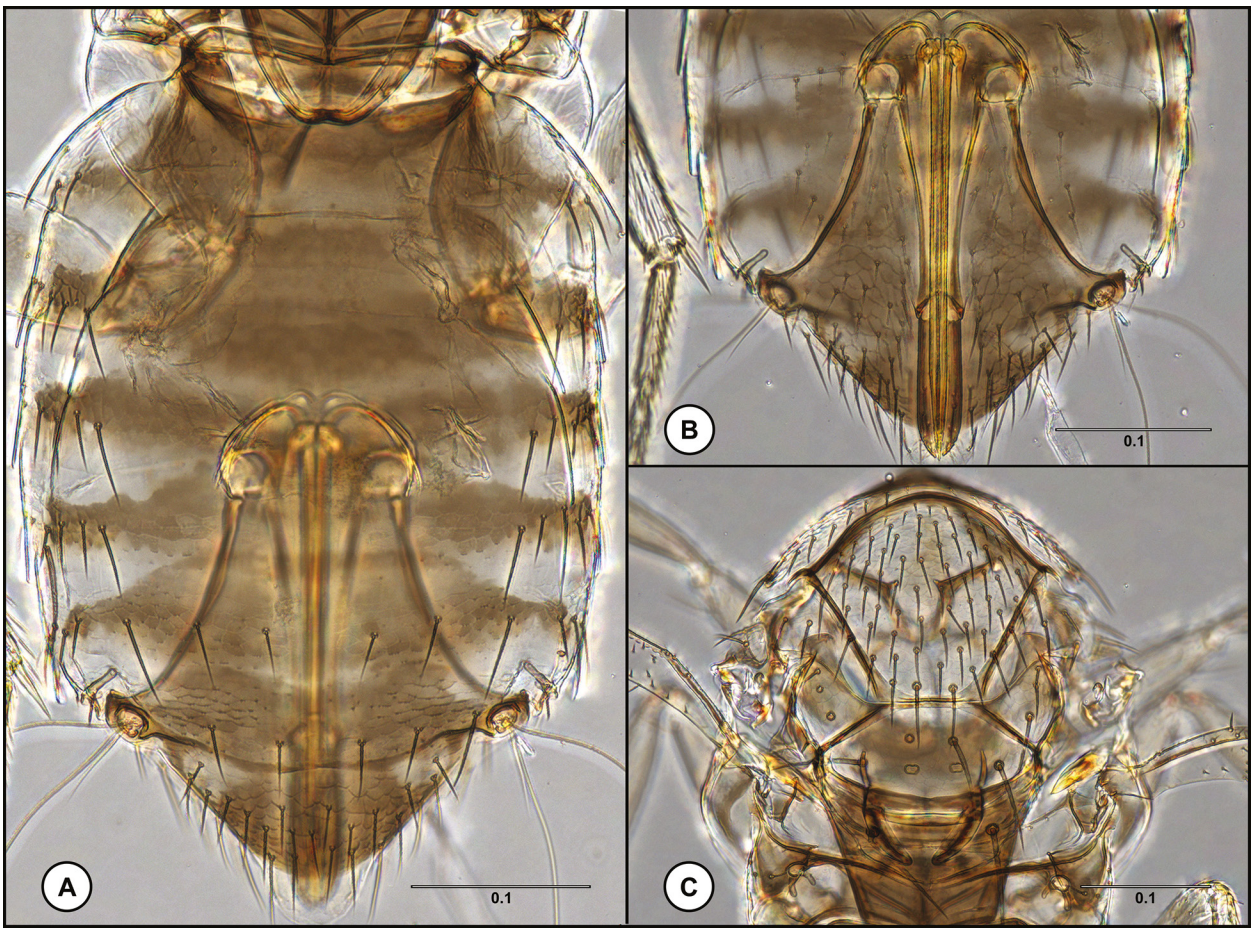


**Figure 2.** *Prococcophagus tobiasi* (Myartseva), female (OSUC 854110). **A)** Metasoma, dorsal view. **B)** Ovipositor, dorsal view. **C)** Mesosoma, dorsal view. Scale bar in millimeters.

recognized species groups of *Coccophagus*, additional species of *Prococcophagus* (sequences are missing for 20 of the 26 described species), the genus *Oenrobia* Hayat, and members of the numerous, undescribed satellite genera for which sequence data exists (A. Polaszek, unpublished data; Z. Lahey, unpublished data). Overall, a concerted phylogenomic approach to the classification of Aphelinidae as a whole is the most palpable way to assess the monophyly of *Prococcophagus*.

Part of the generic diagnosis of *Prococcophagus* is that living and recently killed specimens have an opalescent luster (Kresslein et al. 2025). This feature was first noted by Compere (1936) in his description of *P. aurantifrons* Compere (Fig. 4), where he described the coloration of the head as "pearly white with a bluish luster" and that this feature fades after death. The only other mention of this unusual coloration is by Annecke and Mynhardt (1979) in their treatment of the *Prococcophagus* species of Africa. They were able to observe living specimens of three species, stating that "they all exhibit a distinctive, though pale, bluish white colour in all or almost all parts of the body and antennal scape that, in death – indeed, within an hour or less of death – fade to a pallid whitish hue" (Annecke and Mynhardt 1979). Although the specimens of *P. tobiasi* reported in this study were not seen alive, this feature, unique among aphelinids, was observed for a short time while sorting the specimens from ethanol. Each insect was covered in what can best be described as a film of blue-white opalescence. In agreement with the accounts mentioned above, this color rapidly faded from the body and head, but remained covering the eyes of the insects for significantly longer. The fact that the opalescence fades once the insect is dead eliminates this coloration as a structural feature of the cuticle. Instead, we hypothesize that the opalescence observed on living specimens is the product of glandular secretions that may aid in waterproofing or mate recognition.

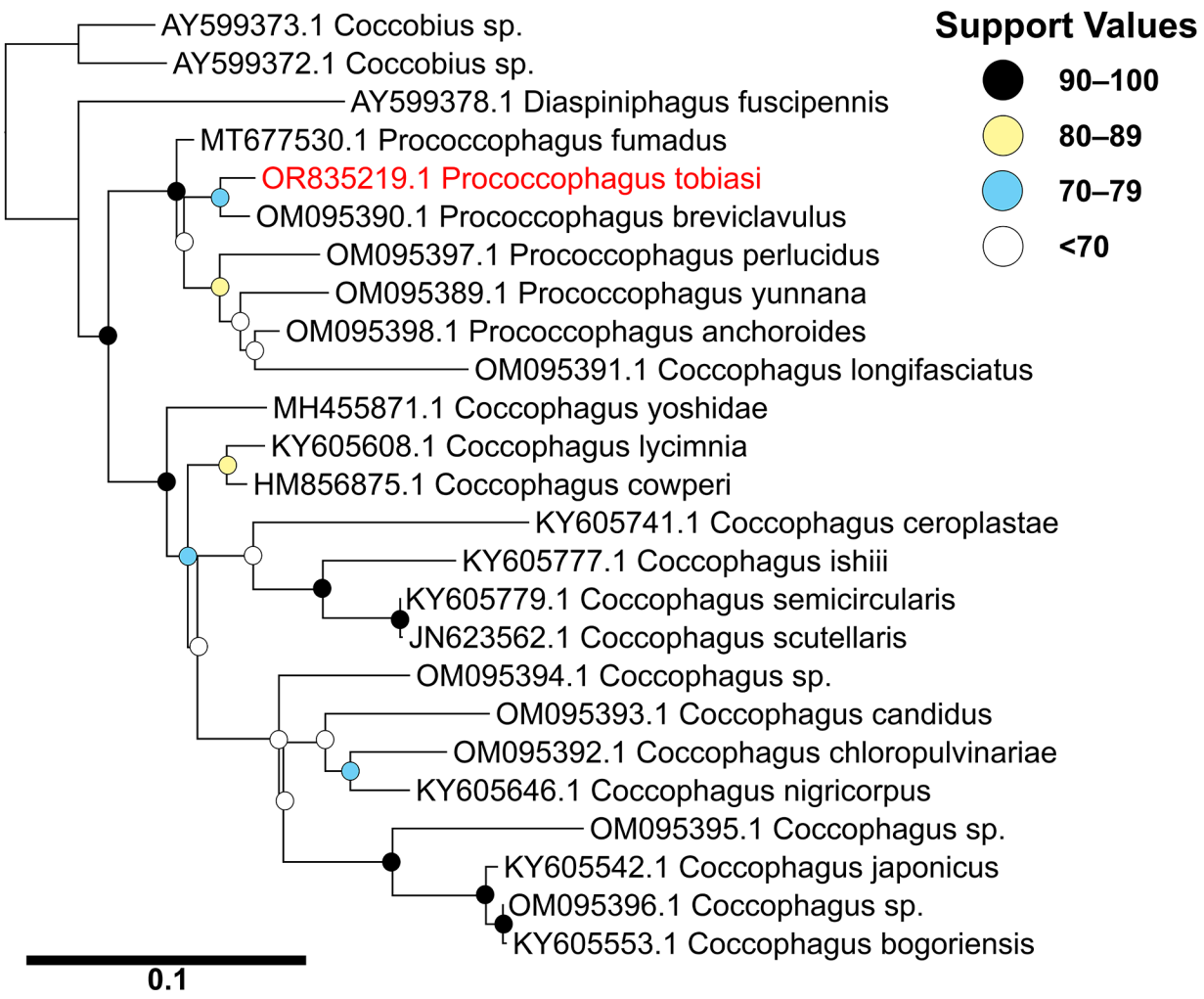


**Figure 3.** Maximum likelihood phylogeny of the 28S-D2-3 region in six *Prococcophagus*, 16 *Coccophagus*, and three outgroup species. The number under the scale bar indicates the number of expected nucleotide substitutions per site. Ultrafast bootstrap support values are indicated by colored circles at nodes.

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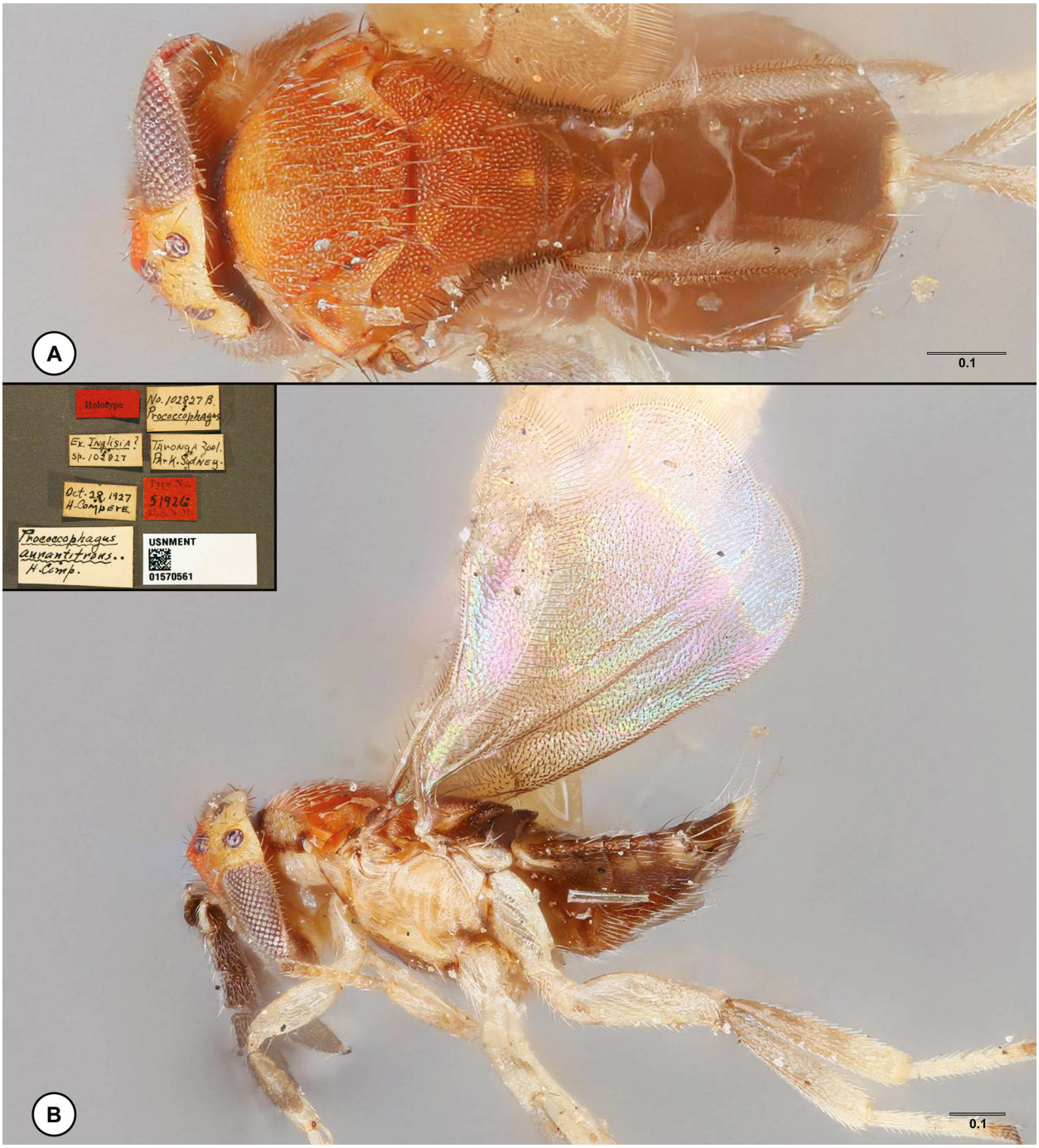


**Figure 4.** *Prococcophagus aurantifrons* Compere, female holotype (USNMENT 01570561). **A)** Habitus, dorsal view. **B)** Habitus, lateral view (inset: specimen labels). Scale bars in millimeters.

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