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Synopeas maximum Awad & Talamas (Hymenoptera, Platygastridae): a new species of parasitoid associated with soybean gall midge, *Resseliella maxima* Gagné (Diptera, Cecidomyiidae)

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Abstract

Synopeas maximum Awad & Talamas, **sp. nov.**, the first reported parasitoid associated with the soybean gall midge, *Resseliella maxima* Gagné, is described based on morphological and molecular data. Parasitoids were reared from soybean stems infested by *R. maxima* in Minnesota. A phylogenetic reconstruction of the genus *Synopeas* Förster was performed with COI sequences (n=2412) available on the Barcode of Life Data System (BOLD). Phylogenetic and barcode gap analyses suggest 279 *Synopeas* species in this dataset, with *S. maximum* sequences forming a monophyletic clade that is distinct from relatives. The *Synopeas maximum* clade was close to specimens from Canada and the United States, suggesting it is native to North America. We present a taxonomic treatment of *S. maximum* to facilitate its identification, including comparison to morphologically similar species. This project provides baseline data for further ecological study of *R. maxima* parasitism, and its management in soybean.

Keywords

gall midge, parasitism, phylogenetic reconstruction, soybean

Introduction

Gall midges (Diptera: Cecidomyiidae) are a hyper-diverse lineage, representing 30% of dipteran diversity in some ecosystems (Huang et al. 2022). Similarly diverse are parasitoids in the subfamily Platygastrinae (Hymenoptera: Platygastridae), (Chen et al. 2021). Platygastrines are larval or egg-larval parasitoids of Cecidomyiidae, and development of the parasitoid is often suspended until the host is in the last instar or prepupal stage (Kim et al. 2011; Abram et al. 2012; Chen et al. 2021). For both Cecidomyiidae and Platygastrinae, the diversity of species far exceeds what has been described (Srivathsan et al. 2022). However, a recent treatment of the genus *Synopeas* from Papua New Guinea, using morphology, DNA barcoding, and available data on host associations, has set a new standard for making inroads into both the taxonomy and ecology of gall midge parasitoids (Awad et al. 2021). The diversity of species and trophic interactions between Cecidomyiidae and Platygastrinae are large and complex. However, agricultural ecosystems can provide excellent opportunities to investigate these relationships within much simpler systems.

In 2018, larvae of an unknown species of cecidomyiid were found associated with dying soybean plants, *Glycine max* (L.) Merr., in the midwestern United States (Gagné et al. 2019). In 2019, this species of unknown origin was described as *Resseliella maxima* Gagné, the soybean gall midge (Gagné et al. 2019). Soybean plants become susceptible to *R. maxima* attack when the plants have two or three expanded trifoliate leaves, which is when the plant stems present natural fissures below the cotyledonary node (McMechan et al. 2021). Adult female midges oviposit in these fissures and the larvae feed within the stem at the base of the plant, resulting in necrotic lesions that can cause lodged, wilted, and dead plants (McMechan et al. 2021; Helton et al. 2022).

Efforts to reduce *R. maxima* injury to soybeans have focused primarily on chemical control, but have so far provided insufficient protection of soybean plants (Hodgson and Helton 2021; McMechan 2021). Therefore, additional tactics for more effective and sustainable management are needed. One potential management approach is biological control, which has yet to be examined for *R. maxima*. Other pestiferous Cecidomyiidae have been successfully managed using biological control agents, including *Aprostocetus epicharmus* (Walker) (Hymenoptera: Eulophidae) that parasitized up to 38% of raspberry cane midge, *Resseliella theobaldi* (Barnes) (Vétek et al. 2006), and *Synopeas myles* (Walker) (Hymenoptera: Platygastridae) that parasitized up to 28% of swede midge, *Contarinia nasturtii* (Kieffer) (Abram et al. 2012b; Ferland 2020).

The present work investigates potential parasitism of *R. maxima* by rearing parasitoids from field-collected soybean stems. We present a taxonomic and molecular description of the *R. maxima*-associated parasitoid, *Synopeas maximum* Awad & Talamas, sp. nov., and a phylogenetic analysis of *Synopeas* sequences available on the Barcode of Life Data System (BOLD).

Methods

Field collection and emergence cages

Soybean stems presenting symptoms of infestation by *R. maxima* (i.e., darkened swollen lesions at the base of the stems) were collected during the summer of 2021 in two fields on one farm near the city of Luverne (Rock County), Minnesota, USA. Field collection started on 30 June 2021, when soybean plants started to show symptoms of infestation, and continued every other week until *R. maxima* larval infestation was no longer detected on 01 September 2021. On each sampling date, 10 randomly selected symptomatic plants were collected per eight sampling locations per field by pulling the entire plant from the soil. These plants were trimmed above the first pair of unifoliate leaves, placed in zipper-locking plastic bags (17.7 × 18.8 cm, Ziploc), and held in coolers until brought to the laboratory (approximately five hours).

In the laboratory, the stems were prepared for placement in emergence cages. The cut end of each stem was wrapped with a small piece of PARAFILM to slow plant dehydration. Soybean roots were trimmed to a length of five centimeters. Ten trimmed stems were placed together in one emergence cage per location. Emergence cages consisted of 5-liter clear plastic paint-mixing buckets with lids (TCP Global Corporation, Lakeside, California, USA). A 6-cm diameter hole was cut in the side of each bucket approximately 6 cm from the bottom of the bucket. A white fine-mesh (0.02 cm mesh size, 100% polyester, Quest Outfitters, Sarasota, Florida, USA) sleeve 30 cm long was attached to the hole with hot glue to allow access to the contents of the cages. The sleeves were tied to prevent insects from escaping. In each cage, the stems were placed vertically into a 3 cm deep layer of potting soil (BM2 Seed Germination and Propagation Mix, Berger, Saint-Modeste, Quebec, CA). The emergence cages were maintained at room temperature in 16h light:8h dark, watered as needed to maintain soil moisture, and checked daily for emergence of insect adults. Adult insects were collected manually into microcentrifuge tubes, freeze-killed in -20 °C for 24 hours and preserved in 95% ethanol for taxonomic and molecular identification.

DNA extraction

Non-destructive DNA extraction from individual specimens followed a modified HotSHOT protocol (Truett et al. 2000). Each specimen was placed in a 0.2 mL PCR tube (Olympus plastic, Cat# 27-125) with 100 µL of the lysis reagent (25 mM NaOH: 0.2 mM disodium EDTA) and incubated at 95 °C for 30 minutes on a Mastercycler nexus PCR cycler (Eppendorf). Samples were cooled to 4 °C and 100 µL of neutralizing reagent (40 mM Tris-HCl) was added to each sample (a final volume of 200 µL). The aqueous solution containing DNA was moved to a fresh tube and 95% Ethanol was added to the specimen for preservation.

DNA barcoding

We barcoded all *Synopeas* (n=16) as well as six adult specimens of *R. maxima* randomly selected from the emergence cages. The cytochrome oxidase subunit I (COI) gene was amplified alongside negative controls using the universal primer pair LCO-1490/HCO-2198 for *S. maximum* and COIA/J-1718 for *R. maxima* (Folmer et al. 1994; Simon et al. 1994; Funk et al. 1995; Gagné et al. 2019). PCR reactions were prepared in a final volume of 20 µL with 1 µL of DNA template, Q5 Hot Start High-Fidelity 2X Master Mix (New England BioLabs), and 500 nM of each primer. Thermalcycling was performed on a Mastercycler nexus PCR cycler (Eppendorf) with an initial denaturation of 2 min at 98 °C, followed by 40 cycles of amplification (10 s at 98 °C, 30 s at 60 °C, and 20 s at 72 °C), and a final elongation of 2 min at 72 °C. The annealing temperature was determined using NEB Tm calculator (version 1.15.0, https://tmcalculator.neb.com/). PCR-products were separated by gel electrophoresis on a 1% agarose gel and imaged under ultraviolet light after staining with GelRed 3X in water (Biotium). PCR-products were cleaned with the Exo-CIP Rapid PCR Cleanup Kit (New England BioLabs) according to manufacturer's instructions and Sanger sequenced in both directions at the University of Minnesota Genomics Center (Saint Paul, Minnesota, USA). Sequences were inspected for peak quality, aligned, and trimmed of priming regions in SnapGene (SnapGene5.3.2).

Synopeas maximum-specific primer design and DNA barcoding

We designed a *Synopeas maximum*-specific forward primer after finding that (1) not all *Synopeas* samples were compatible with the LCO-1490/HCO-2198 primer set, and (2) *Synopeas* samples that were amplified with LCO-1490/HCO-2198 primers typically generated low sequence quality when sequencing from the LCO-1490 primer (these sequences were ~50% of the amplicon length and were low quality, with average quality scores around 20, rather than a typical mean of ~40). Using the preliminary data from the reverse reads, we selected a new forward primer targeting a region that was conserved across our samples (SYN_F: 5'-CGATTAGAAGTTGGAACTCC-3') and generated a 550-bp amplicon when combined with the HCO-2198 reverse primer. A new PCR reaction mix was prepared for all wasps (n=16) as described in the section above, using the new primer pair (SYN_F/HCO-2198). Thermal cycling was performed on a Mastercycler nexus PCR cycler (Eppendorf) with an initial denaturation of 2 min at 98 °C, followed by 35 cycles of amplification (10 s at 98 °C, 30 s at 61 °C, and 20 s at 72 °C), and a final elongation of 2 min at 72 °C.New PCR-products were separated, purified, and sequenced as described above. Resulting sequences were uploaded to BOLD and are listed in Table 1.

Phylogenetic reconstruction

A phylogenetic analysis was performed with *Synopeas* sequences available on BOLD (Suppl. material 1) along with *S. maximum* sequences, and selected outgroups (n=2412). Amino acid sequences were aligned with MAFFT version 7.475 (Katoh and Standley 2013) using default parameters for downstream use in phylogenetic analyses.

Table 1. Specimens of *Synopeas maximum* reared from emergence cages.

Lab code†	Collecting unit identifier	Sex	BOLD ID
PG01	FSCA 00095876	Male	SYMAX005-23
PG02	FSCA 00095877	Male	SYMAX006-23
PG03	FSCA 00095878	Male	SYMAX011-23
PG04	FSCA 00095879	Male	SYMAX010-23
PG05	FSCA 00095880	Female	SYMAX009-23
PG06	FSCA 00095881	Female	SYMAX001-23
PG07	FSCA 00095882	Male	SYMAX002-23
PG08	FSCA 00095883	Female	SYMAX003-23
PG10	FSCA 00095885	Female	SYMAX012-23
PG11	FSCA 00060750	Male	SYMAX013-23
PG12	FSCA 00060752	Female	SYMAX014-23
PG13	FSCA 00060751	Male	SYMAX004-23
PG17	FSCA 00060754	Female	SYMAX016-23
PG18	FSCA 00060755	Male	SYMAX007-23
PG20	FSCA 00060756	Male	SYMAX008-23
PG21	FSCA 00060757	Female	SYMAX017-23

†Codes used in phylogenetic tree (Suppl. material 3 and Fig. 7).

The alignment was trimmed in SnapGene (SnapGene5.3.2) to remove sequences from outside of the SYN_F/HCO-2198 amplicon. A reduced version of the alignment, which excluded identical sequences (n=1459, 518 bp in length), was submitted to maximum likelihood analysis in RAxML version 8.2.11 using a GTRGAMMA substitution model and 1000 bootstrap replicates (Stamatakis 2014). Tree topology was rooted and visualized in FigTree version 1.4.4 and annotated in Inkscape version 1.2.1. Species delimitation was performed with the ASAP web server and default settings (https://bioinfo.mnhn.fr/abi/public/asap/) including the full aligned FASTA file containing all sequences (n=2412) and a JC69 Jukes-Cantor substitution model (Puillandre et al. 2021). The best scoring partition was selected for downstream processing as per ASAP guidance.

Imaging

Photography was performed using a Macropod microphotography system (Macroscopic Solutions) using 10X and 20X Mitutoyo objective lenses, with image stacks rendered in Helicon Focus. Images of primary types were deposited in Zenodo (Table 2), and images of molecular voucher specimens were deposited in BOLD.

Institutional abbreviations

Specimens examined during this study are deposited in the following institutions and abbreviated as follows:

CNCI	Canadian National Collection of Insects, Ottawa, Canada;
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, USA;

HMNH	Hungarian Museum of Natural History, Budapest, Hungary;
MEFS	Museo Entomologico Filippo Silvestri, Portici, Italy;
MZH	Finnish Museum of Natural History, Helsinki, Finland;
MZLU	Biological Museum Lund University, Lund, Sweden;
NHMD	Natural History Museum Denmark, Copenhagen, Denmark;
NHMO	Zoological Museum, University of Oslo, Oslo, Norway;
NHMUK	Natural History Museum, London, UK;
NHMW	Naturhistorisches Museum Wien, Vienna, Austria;
NIAS	National Institute of Agricultural Sciences, Jeonju, South Korea;
NMINH	National Museum of Ireland, Dublin, Ireland;
OOLL	Oberösterreichische Landesmuseum Linz, Austria;
RMNH	Naturalis Biodiversity Center, Leiden, Netherlands;
UMSP	University of Minnesota, St. Paul, Minnesota, USA;
USNM	United States National Museum, Washington, DC, USA;
ZMUN	Natural History Museum, University of Oslo, Norway.

Table 2. *Synopeas* species in the *rhanis* species group.

Species	Type repository	Type locality	Images
S. basipubens Buhl, 2014	NHMD	Togo	
S. bialowiezaensis Buhl, 2005	MZH	Poland	
S. bouceki Buhl, 2007	NHMUK	India	
S. convexum Thomson, 1859	MZLU	Sweden	https://www.flickr.com/search/?tags=MZLUTYPE02851
S. cynipsiphilum (Ashmead, 1887)	USNM	USA	https://zenodo.org/record/7662443#.Y_Up1HbMJaQ
S. decurvatum (Nees von Esenbeck, 1834)	type lost	Germany	
S. dentiscutum (Szabo, 1981)	HMNH	Hungary	https://doi.org/10.5281/zenodo.7585486
S. epigeios Buhl, 2006	NHMD	Denmark	
S. flavicorne (Ashmead, 1893)	USNM	USA	https://zenodo.org/record/7662438#.Y_Uoy3bMJaQ
S. gibberosum Buhl, 1997	ZMUN	Norway	https://zenodo.org/record/7591619#.Y9mCmnbMJaQ
S. hyllus (Walker, 1835)	NMINH	Ireland	https://zenodo.org/record/7591590#.Y9l_AHbMJaQ
S. kimi Choi & Buhl, 2006	NIAS	South Korea	
S. maximum Awad & Talamas, 2023	FSCA	USA	https://zenodo.org/deposit/7662387
S. oleae Buhl & Viggiani, 2008	MEFS, paratypes in NHMD	Italy	
S. politiventre Buhl, 2015	NHMD	Chile	
S. prospectum Förster, 1861	NHMW	Switzerland	https://zenodo.org/record/7591572#.Y9l9cnbMJaQ
S. protuberatus Buhl, 2009	RMNH	Vietnam	
S. rhanis (Walker, 1835)	NMINH	England	https://zenodo.org/record/7442827#.Y9l-M3bMJaQ
S. sheldrakei Buhl, 2014	MZLU	Sri Lanka	
S. subtilis Buhl, 2004	HMNH	Mongolia	
S. talhouki Vlug, 1976	Vlug collection, paratypes in USNM, HMNH, NHMW	Lebanon	https://zenodo.org/record/7662450#.Y_UxlnbMJaQ
S. thailandicum Buhl, 2007	OOLL	Thailand	
S. triangulatum Buhl, 2014	NHMD	Australia	
S. tuberosum Sundholm, 1970	MZLU	South Africa	
S. veenakumariae Buhl, 2014	MZLU	Sri Lanka	
S. vietnamianus Buhl, 2009	RMNH	Vietnam	

Results

Emergence cages

We collected 2221 adults of *R. maxima*. Other cecidomyiids collected from the cages included two individuals of *Lestodiplosis* spp. Two taxa of parasitoids were collected from the cages, including 16 individuals of *S. maximum* and 4 individuals of *Aphanogmus* sp. (Ceraphronidae).

DNA Barcoding

We performed DNA barcoding on each of the 16 *Synopeas* adults recovered from emergence cages (Table 1). COI sequences from these specimens had greater than 98% sequence similarity to each other but no close matches on GenBank. The most similar was a specimen identified as Platygastrinae sp., (GenBank ID MG501619.1, 97% query cover, 89.6% nucleotide identity), collected in Banff National Park, Alberta, Canada. Unfortunately, there are no photographic records of this specimen and a morphological comparison was not possible. We also verified the identity of randomly selected gall midges that emerged from the cages. The specimens were morphologically identified as *R. maxima*, had identical nucleotide sequences to each other, and a 97.67% sequence similarity to a *R. maxima* specimen from Nebraska, USA (accession number LC437340.1).

Systematics of *Synopeas*

The generic concept of *Synopeas* is rather straightforward, and it can be separated from other platygastrines by the fusion of T1–T2 and S1–S2 (Jackson 1969; Awad et al. 2021). However, taxonomic structure within the genus is essentially non-existent. Given that *Synopeas* includes over 350 species, this presents a significant challenge for species identification (Awad et al. 2021). This situation is exacerbated by the spread of numerous species by human activities, requiring revision of the world fauna to be certain that a species was not previously described. Our ability to ascertain if *S. maximum* is adventive is presently limited to the use of DNA barcode libraries, and comparison to type specimens that are in the morphological vicinity of *S. maximum*. So far, neither of these approaches have provided a match. Our efforts are not exhaustive, nor is it currently feasible to examine type material for all described species of *Synopeas*. Fortunately, *S. maximum* has a distinctive characteristic shared by a minority of species: a deep scuto-scutellar sulcus (i.e., deep divide between the mesoscutum and mesoscutellum) (Fig. 6C, D). This eliminates the need for comparison to the vast majority of described *Synopeas*. Within the Nearctic region, primary type images provided by Talamas et al. (2017) yielded only two species, *S. cynipsiphilum* (Ashmead) and *S. flavicorne* (Ashmead), with the mesosomal structure found in *S. maximum*. Given that the soybean gall midge is an emerging pest, we also considered it possible that *S. maximum* represents an adventive population, derived from a distribution outside of the United States. Our literature search and examination of type specimens found other species with the deeply divided mesosoma, but not a species-level match. Because the mesosomal divide creates such a distinctive "hunchbacked" appearance, we consider that it has high value as a diagnostic character and use it to define the *rhanis*-group of *Synopeas*, named for *S. rhanis* (Walker, 1835), which was the earliest described species with this character. The *rhanis*-group includes 26 species (Table 2) that we consider to be worth comparing to *S. maximum*. We selected five species from this group for closer examination and comparison, based on morphological similarity and occurrence in cold temperate climates. However, all species of the *rhanis*-group were considered and compared to the new species using type images or published descriptions.

***Synopeas cynipsiphilum* (Ashmead)**
Fig. 1

Leptacis cynipsiphila Ashmead, 1887: 129 (original description); Fouts 1924: 117, 128 (description, lectotype designation, keyed).
Leptacis cynipsiphilus Ashmead, 1893: 271, 274 (description, spelling error, keyed).
Leptacis cynipiphila Ashmead: Kieffer 1926: 637, 646 (description, spelling error, keyed).
Synopeas cynipsiphilum (Ashmead): Masner 1967: 303 (generic transfer); Masner and Muesebeck 1968: 99 (type information); Vlug 1995: 77 (cataloged, type information).

***Synopeas flavicorne* (Ashmead)**

Leptacis flavicornis Ashmead, 1893: 275 (original description); Fouts 1924: 117, 128 (description, type designation, keyed).
Amblyaspis flavicornis (Ashmead): Brues 1916: 532, 533 (generic transfer, description, keyed).
Synopeas flavicorne (Ashmead): Masner and Muesebeck 1968: 99 (generic transfer, type information, emendation).

***Synopeas gibberosum* Buhl**
Fig. 2

Synopeas gibberosus Buhl, 1997: 439 (original description); Buhl 1999: 39 (keyed); Buhl and Choi 2006: 133 (keyed).
Synopeas gibberosum Buhl: Buhl and Notton 2009: 1696 (cataloged, distribution, emendation); Buhl and O'Connor 2010: 4 (distribution).

Figure 1A–E. *Synopeas cynipsiphilum*, female (FSCA 00097487) **A** head, anterior view **B** head and mesosoma, dorsal view **C** head and mesosoma, ventrolateral view **D** head and mesosoma, lateral view **E** mesosoma and metasoma, dorsal view.

Synopeas prospectum Förster
Fig. 3

Synopeas prospectus Förster, 1861: 41 (original description); Dalla Torre 1885: 78 (reprint of Förster (1861)); Kieffer 1926: 668, 680 (description, keyed); Vlug 1973: 179 (lectotype designation); Vlug 1995: 81 (cataloged, type information); Buhl 1997: 27 (description).

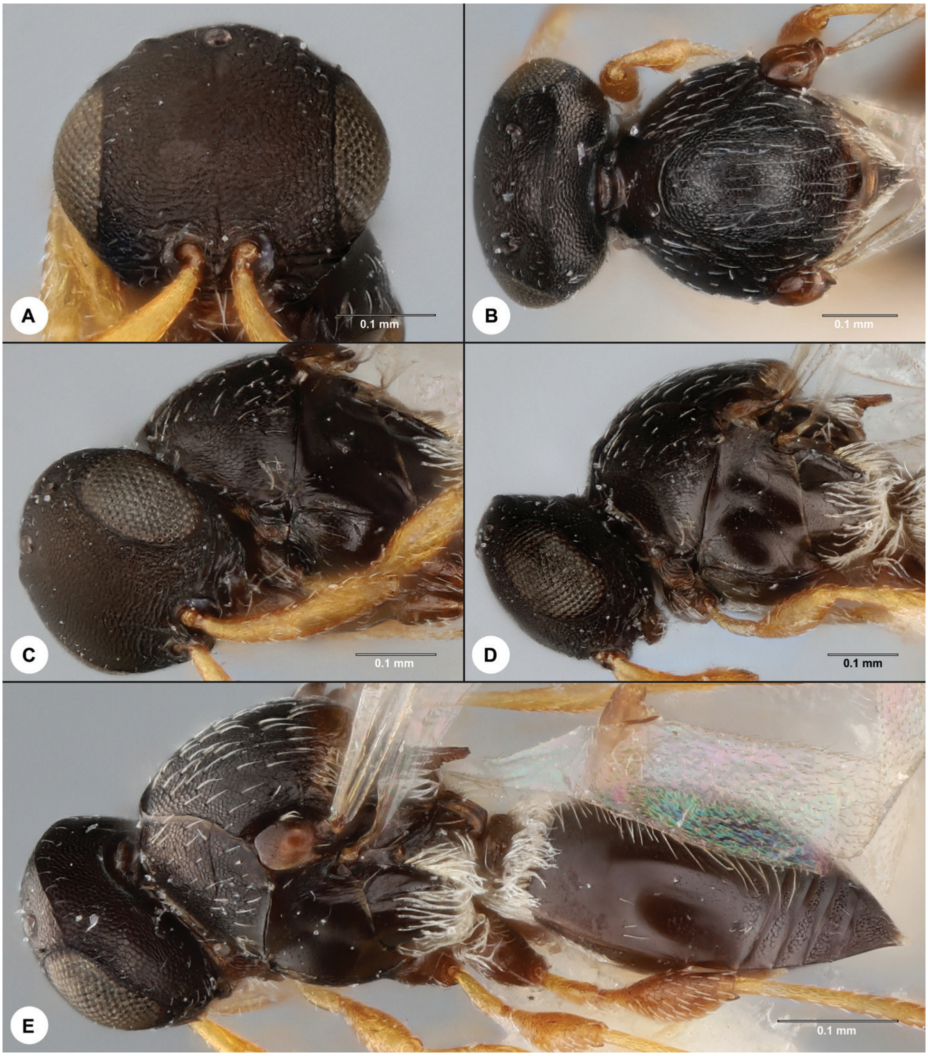

Figure 2A–E. *Synopeas gibberosum*, holotype female (NHMO 0001) **A** head, anterior view **B** head and mesosoma, dorsal view **C** head and mesosoma, ventrolateral view **D** head and mesosoma, lateral view **E** habitus, dorsolateral view.

Synopeas Prospectus Förster: Kieffer 1914: 419 (description).

Synopeas (*Synopeas*) *prospectus* Förster: Kieffer 1916: 554, 555 (description, subgeneric assignment, keyed).

Synopeas rhanis **(Walker)**

Fig. 4

Platygaster Rhanis Walker, 1836: 225 (original description).

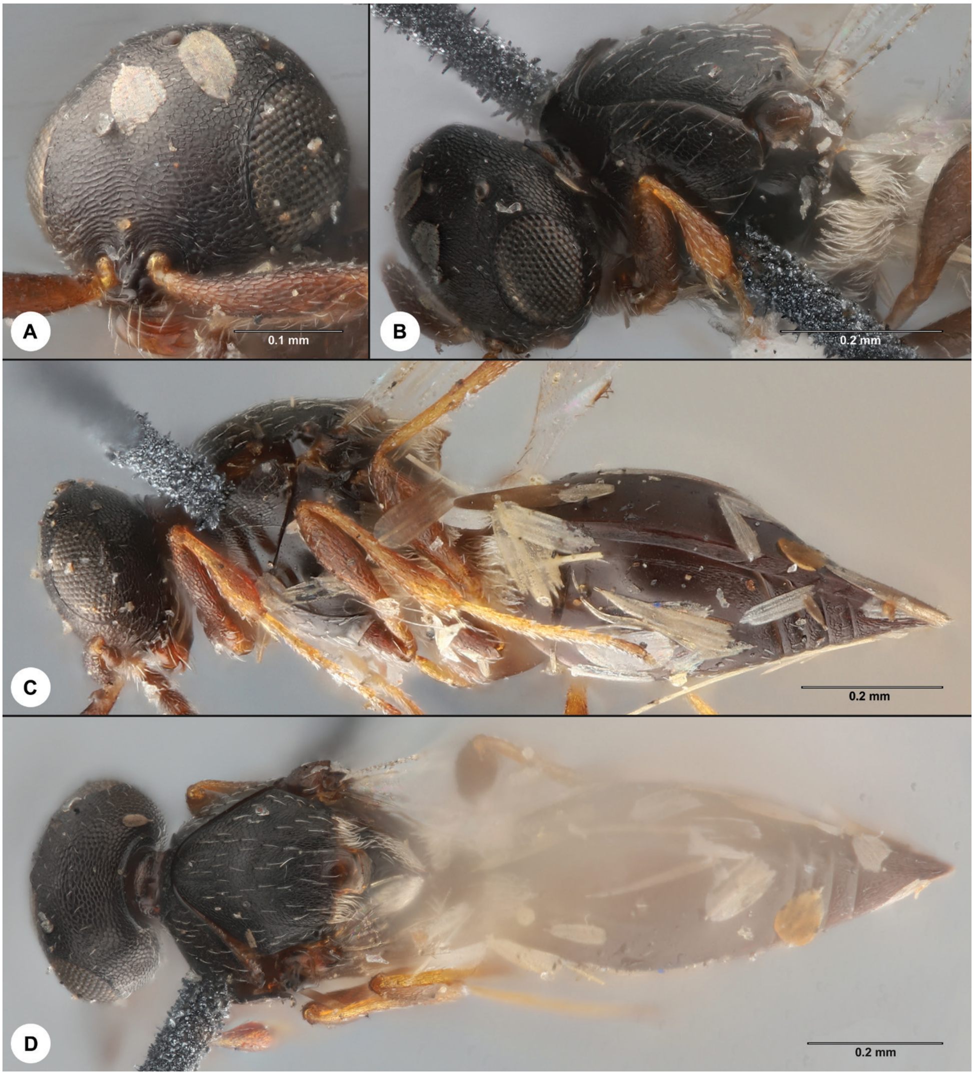

Figure 3A–D. *Synopeas prospectum*, lectotype female (NHMW-HYM #0005306) **A** head, anterolateral view **B** head and mesosoma, dorsolateral view **C** habitus, lateral view **D** habitus, dorsal view.

Platygaster Acco Walker, 1836: 229 (original description. Synonymized by Vlug (1985)); Vlug 1985: 209 (junior synonym of Synopeas rhanis (Walker)).

Synopeas Acco (Walker): Marshall 1873: 19 (generic transfer); Kieffer 1914: 427 (description).

Synopeas Rhanis (Walker): Marshall 1873: 19 (generic transfer); Kieffer 1914: 341 (description of adult and immature stages).

Synopeas rhanis (Walker): Kieffer 1906: 134 (description); Kieffer 1926: 668, 676 (description, keyed); Masner 1965: 142 (type information); Vlug and Graham 1984: 130 (lectotype designation); Vlug 1985: 209 (description of type, keyed); Vlug

1995: 81 (cataloged, type information); Buhl 1999: 39 (keyed); MacGown and Evans 2003: 6 (description); O'Connor, Nash, Notton and Fergusson 2004: 24 (catalog of Irish species); Buhl and Notton 2009: 1698 (cataloged, distribution); Buhl and O'Connor 2010: 14 (distribution).

Synopeas acco (Walker): Kieffer 1926: 669, 683 (description, keyed); Vlug and Graham 1984: 129 (lectotype designation); Vlug 1985: 209 (description of type, keyed); Vlug 1995: 75 (type information); O'Connor, Nash, Notton and Fergusson 2004: 24 (type information, catalog of Irish species).

Synopeas ?rhanis (Walker): Buhl and Choi 2006: 133, 135 (keyed, distribution in Korea).

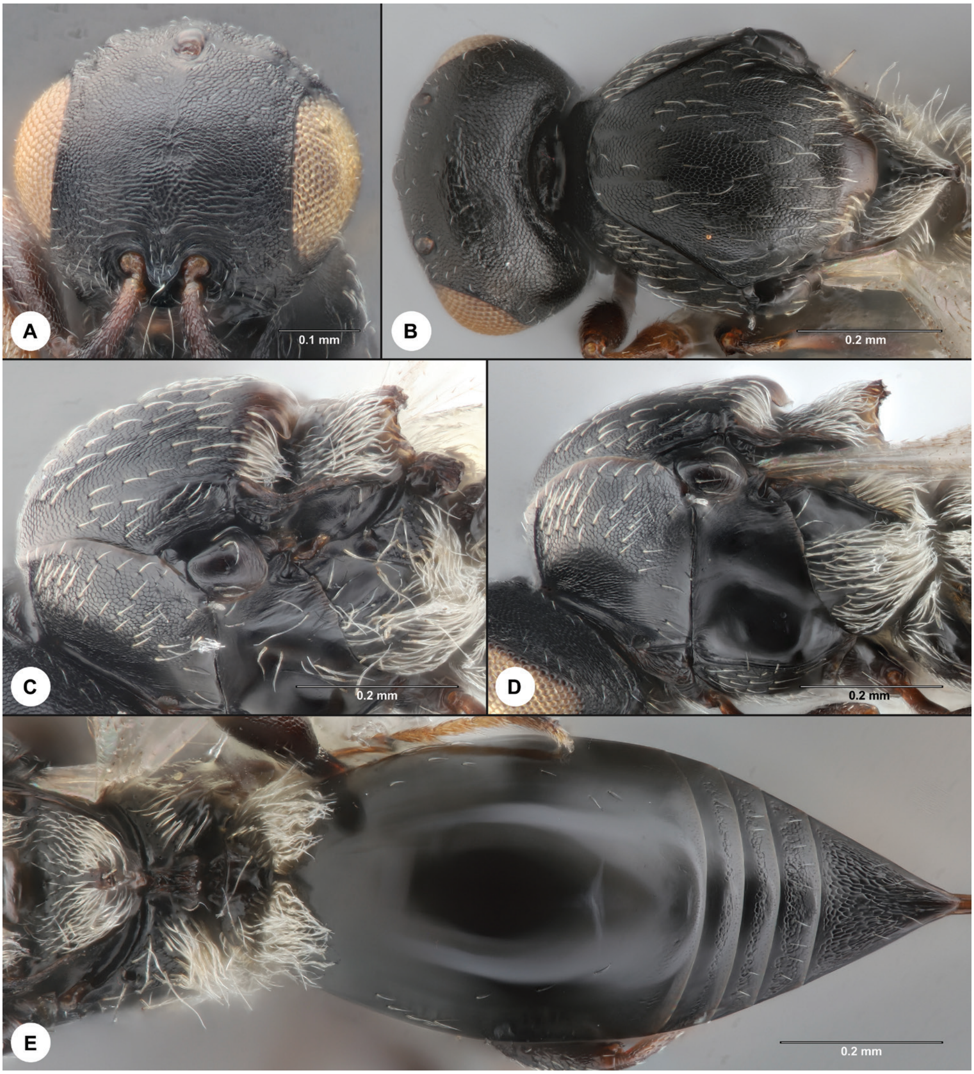

Figure 4A–E. *Synopeas rhanis*, female (FSCA 00034191) **A** head, anterior view **B** head and mesosoma, dorsal view **C** mesosoma, dorsolateral view **D** mesosoma, lateral view **E** mesosoma and metasoma, dorsal view.

Synopeas maximum **Awad & Talamas, sp. nov.**

https://zoobank.org/74487E47-EB76-4899-8A22-F91906954842

Figs 5, 6

Description. Females. *Body length*: 1.4–1.7 mm. ***Body color*:** black. ***Color of legs*:** coxae dark brown, otherwise yellow to dark brown. ***Color of mesoscutellar spine*:** concolorous with mesoscutellar disc.

***Head*.** Shape of head in anterior view: ovoid. Central keel: absent; present only between toruli. Sculpture on frons: reticulate microsculpture. Epitorular sculpture: reticulate microsculpture; minute rugulae. Number of clypeal setae: 4. Length of median pair of clypeal setae: longer than lateral pair. Arrangement of clypeal setae: evenly spaced. Shape of mandible: bidentate. Distance between lateral ocellus and compound eye (OOL): approximately 1 ocellar diameter. OOL: LOL: 1:2. Lateral ocellar depression: present posterolaterally. Hyperoccipital carina: present between lateral ocelli. Hyperoccipital carina strength: fine, laterally weakened. Distance between lateral ocellus and hyperoccipital carina: approximately 1 ocellar diameter. Female antenna with 3 clavomeres, claval formula 1-1-1.

***Mesosoma*.** Epomial carina: present, complete, or nearly so. Microsculpture of lateral pronotum: present anterodorsally, absent posteroventrally. Lateral pronotal sculpture coverage: more than ¾. Setation of lateral pronotum: anteroventrally glabrous, otherwise uniformly sparse (Figs 5, 6D). Mesoscutellar spine: short and pointed. Mesoscutellar spine in lateral view: pointing posteriorly; slightly upcurved at tip. Posterior margin of propodeal carina in lateral view: rounded. Mesosomal dorsum in lateral view: slightly convex. Scuto-scutellar sulcus: deep, causing mesoscutum to be elevated relative to mesoscutellum. Notauli: unmarked or faintly indicated. Parapsidal line: very faint. Setation of mesoscutum: sparse (Fig. 6B). Mesoscutal lamella: broad and rounded. Setation of mesoscutellum: anteromedially absent, posterolaterally dense.

***Metasoma*.** Microsculpture of S2: absent; faint narrow bands in lateral portion of posterior margin. Shape of S2: medioventrally expanded. Sculpture of T2: absent. Length of T2: approximately as long as mesosoma. Sculpture of S3 to S5: reticulate. Sculpture of S6: entirely reticulate. Sculpture of T6: entirely reticulate. Shape of T6: triangular, longer than wide.

***Wing*.** Length of setae on disc of fore wing: shorter than distance between setal bases. Density of setae on disc of fore wing: moderately dense. Arrangement of setae on disc of fore wing: uniformly setose distally, proximally glabrous with linea setosa. Fore wing marginal setae: uniformly very short.

Males. *Body length*: 1.1 to 1.3 mm. Identical to females except for metasoma and antenna.

***Antenna*.** Setation: A1 and A2 with few scattered setae, A3 to A10 with long, uniformly dense setae. A2 in lateral view: slightly longer than wide, distally widened forming a “teardrop” shape. A3: round, about half the size of A2 or A4. A4: roughly cylindrical, about twice as long as wide. A5 in lateral view: about half as long as A4, proximally widened. A6 to A9: roughly ovoid, wider in lateral view than in anterior view, A6 slightly smaller than following antennomeres. A10: about twice as long as wide.

Figure 5. *Synopeas maximum* Awad & Talamas, sp. nov., holotype, female (FSCA 00095883), lateral habitus.

Metasoma. Microsculpture of S2: narrow band at posterior margin. Sculpture of T2: absent; narrow transverse band of microsculpture at posterior margin. Length of T2: approximately as long as mesosoma, or shorter.

Material examined. ***Holotype*:** USA • ♀; Minnesota, Luverne; 43.605889°N, 96.275111°W; 30.VI–30.VII.2021; Gloria Melotto leg.; *Resseliella maxima* on soybean; FSCA 00095883 (FSCA).

***Paratypes*:** USA • 1♀1♂; same collection data as for preceding; VI–VII.2021; FSCA 00095881 to 00095882 (CNCI) • 3♀3♂; same collection data as for preceding; VI–VIII.2021; FSCA 00060750 to 00060754 (FSCA) • 1♀3♂; same collection data as for preceding; VI–VII.2021; FSCA 00095876 to 00095878, 00095885 (UMSP) • 1♀2♂; same collection data as for preceding; VIII–XII.2021; FSCA 00060755 to 00060757 (UMSP) • 1♀1♂; same collection data as for preceding; VI–VII.2021; FSCA 00095879 to 00095880 (USNM).

Etymology. The species epithet refers to the ecological association with soybean gall midge, *Resseliella maxima* Gagné, and soybean, *Glycine max* (L.) Merr.

Diagnosis. *Synopeas maximum* can be separated from other species in the *rhanis* group by the following combination of characters: scuto-scutellar sulcus deep, causing mesoscutum to be elevated relative to mesoscutellum; hyperoccipital carina present

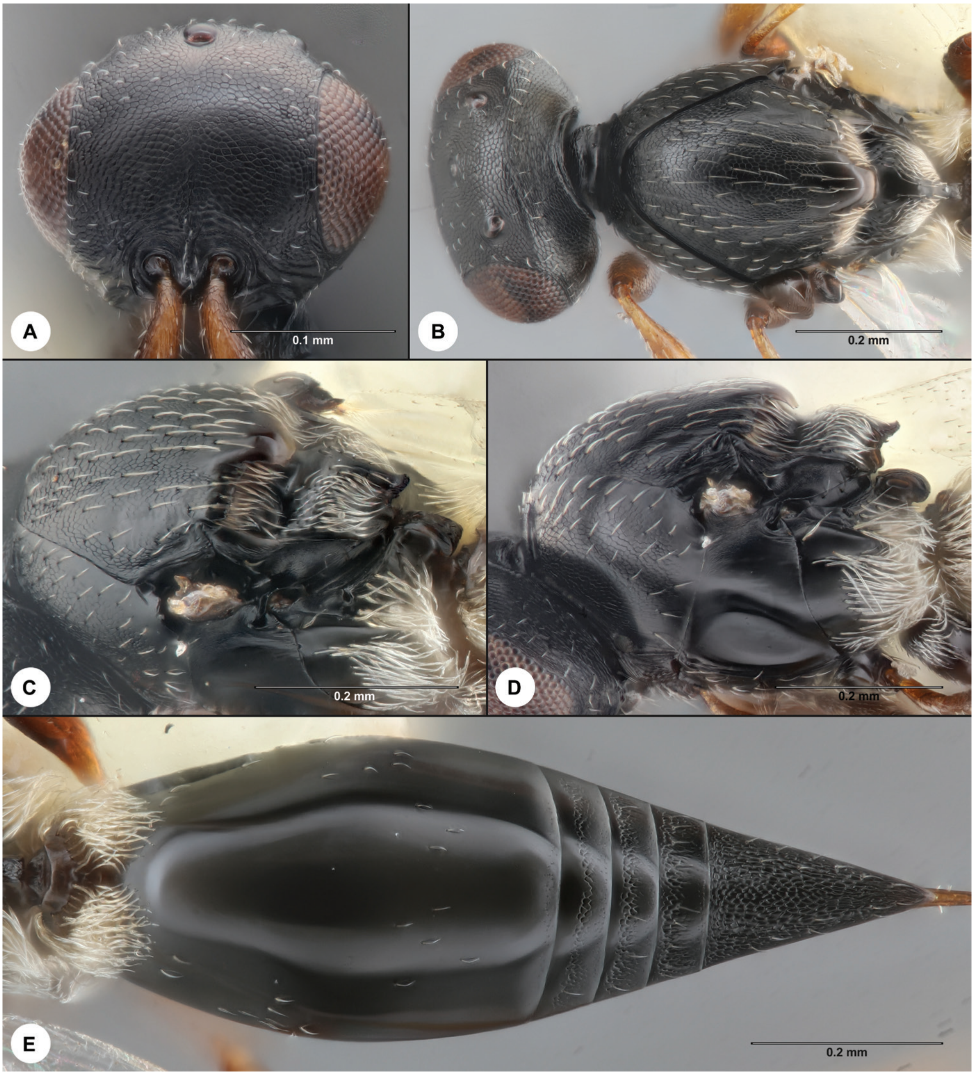

Figure 6A–E. *Synopeas maximum*, female **A** head, anterior view (FSCA 00095883) **B** head and mesosoma (FSCA 00095881) **C** mesosoma, dorsolateral view (FSCA 00095883) **D** mesosoma, lateral view (FSCA 00095883) **E** metasoma, dorsal view (FSCA 00095881).

between lateral ocelli, laterally weakened; mesoscutellar spine short, pointing posteriorly, sometimes with a slight upturn at the tip, but always originating from below the dorsal apex of the mesoscutellum (separating it from *S. gibberosum*, *S. prospectum*, and *S. rhanis*); female S2 expanded ventromedially, with microsculpture absent or very faint; female S6 and T6 entirely sculptured, triangular, about 2 times as long as wide. The latter character is very useful for separating *S. maximum* from *S. cynipsiphilum* and *S. flavicorne*, in which female T6 is wider than long.

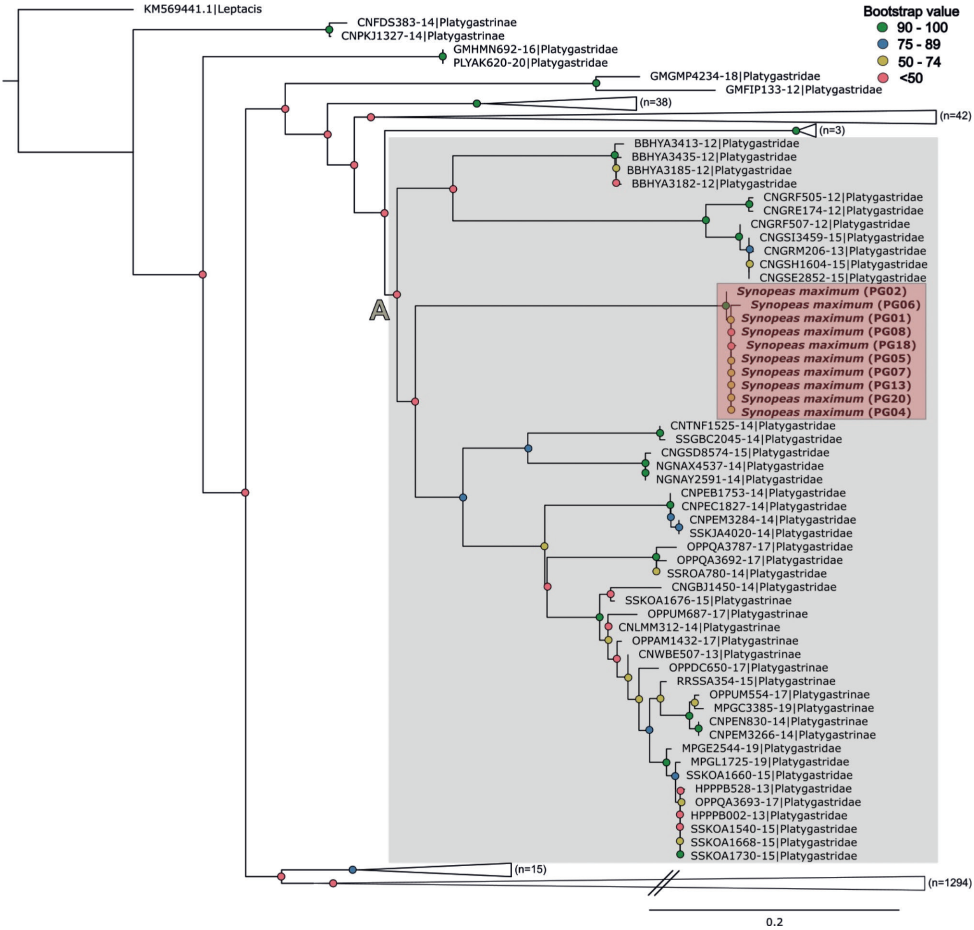

Figure 7. Simplified phylogenetic tree of the genus *Synopeas*. Maximum likelihood analyses were used to reconstruct a *Synopeas* phylogeny. This reduced version focuses on *S. maximum* (red box) and its closest relatives in clade A (gray box). Node circles are color coded to indicate bootstrap support. Specimens are named with sequence ID and taxon originated from BOLD. The full tree can be found in Suppl. material 3.

Phylogenetic reconstruction

The tree in Fig. 7 is a simplified version of the full consensus tree (Suppl. materials 3, 4) that comprises all the COI sequences derived from putative *Synopeas* sp. available in BOLD (excluding duplicates) wherein clades not relevant to species-level treatment of *S. maximum* were collapsed. While the backbone largely has lower bootstrap support (<50%), many species or putative species groups are strongly supported. ASAP analysis for species delimitation defined a total of 279 putative *Synopeas* species with 0.024 threshold distance (Suppl. material 5). Additionally, all *S. maximum* sequences were clustered into a single putative species by ASAP (Suppl. material 2).

We used the phylogenetic reconstruction (Fig. 7) to infer *S. maximum* relationships and origin. Specimens in clade A are all from Canada (n=37) and the northern

United States (n=7), suggesting that *S. maximum* is also native to North America. However, not all specimens in clade A belong to the *rhanis* group, and some representatives of the *rhanis* group are outside of clade A. Our analysis does not support the monophyly of the *rhanis* group, although the deep scuto-scutellar sulcus is still useful for identification.

Discussion

The goal of the emergence cages was to obtain *R. maxima* and potential parasitoids of cecidomyiid agricultural pests. In addition to *R. maxima*, the only other cecidiomyiids collected were two individuals identified as *Lestodiplosis* spp., which are known to be predaceous (Gagné and Jaschhof 2017). Although we detected emergence of two hymenopteran parasitoid species (i.e., 4 individuals of *Aphanogmus* sp. and 16 individuals of *S. maximum*) in our emergence cages, we focused our investigations only on *S. maximum* for several reasons. Species from the genus *Aphanogmus* are primarily hyperparasitoids (Polaszek and Dessart 1996; Jaramillo and Vega 2009; Hofsvang et al. 2014; Pérez-Rodríguez et al. 2019) or parasitoids of predaceous cecidomyiids (Gilkeson et al. 1993; Matsuo et al. 2016), while *Synopeas* is a genus that is known to parasitize only cecidomyiids (Awad et al. 2021). However, the role of *Aphanogmus* sp. in this system needs further investigation.

Platygastrinae are important natural enemies of cecidomyiids (Austin 1984; Kim et al. 2011; Johnson et al. 2013; Chavalle et al. 2015). The recent emergence and spread of *R. maxima* and several other cecidomyiids, such as *Contarinia nasturtii* Kieffer (Philips et al. 2017), *Contarinia brassicola* Rondani (Mori et al. 2019) and *Chilophaga virgati* Gagné (Calles Torrez et al. 2014), poses a threat to agriculture in the northern U.S. and Canada. To improve management for these and other cecidomyiids that may emerge as pests in the future, further work on the ecological relationships and taxonomy of *Synopeas* and other Platygastrinae is required.

Here, morphological assessments grouped *S. maximum* with the *rhanis*-group (i.e., "hunchbacked" appearance) which facilitates its identification. Although the *rhanis*-group did not form a monophyletic clade in molecular analyses, this feature appears to be useful for diagnostics. Additionally, we discovered that *S. maximum* clustered with other putative *Synopeas* species collected from Canada and the United States, suggesting that *S. maximum* may be native to North America.

Different methods for assessing parasitism of midges have been described, including rearing of field-collected hosts in the laboratory (Abram et al. 2012b), PCR-based molecular methods (Greenstone 2006; Magagnoli et al. 2022), and host dissections (Roubos and Liburd 2013). Here, we opted to rear out putative natural enemies of *R. maxima* because host dissections would not provide us with adults for taxonomic identification, and PCR-based molecular methods were impractical since we did not want to make assumptions about putative parasitoids that might be present. Our results suggest that *S. maximum* is likely a primary parasitoid of *R. maxima* because (1) it was reared out of emergence cages with field-collected soybean stems heavily infested with *R. maxima* and (2) the genus *Synopeas* is known to exclusively parasitize Cecidomyiidae. However, additional research is needed to confirm that *S. maximum* is indeed a parasitoid of *R. maxima*. Furthermore, the potential impact of *S. maximum* as a biological control agent of *R. maxima* is still unknown and more research needs to be performed in this area.

With the known geographic range of *R. maxima* expanding (McMechan et al. 2021), sustainable methods to manage this pest, such as biological control, need to be explored. As taxonomic work is foundational to the introduction, conservation, and augmentation of natural enemies (de Moraes 1987), the description of *S. maximum* will facilitate future research on the biological control of *R. maxima*.

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Supplementary material 1

CSV file with BOLD bins for putative *Synopeas* sequences

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Data type: table

Link: https://doi.org/10.3897/jhr.96.102865.suppl1

Supplementary material 2

ASAP partitions

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Data type: PDF file

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Supplementary material 3

Full phylogenetic reconstruction of *Synopeas*

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Data type: PDF file

Link: https://doi.org/10.3897/jhr.96.102865.suppl3

Supplementary material 4

Newick file for full phylogenetic reconstruction of *Synopeas*

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Data type: text file

Link: https://doi.org/10.3897/jhr.96.102865.suppl4

Supplementary material 5

Full ASAP results

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