

Field studies and molecular forensics identify a new association: *Idris elba* Talamas, sp. nov. parasitizes the eggs of *Bagrada hilaris* (Burmeister)

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Abstract

A species of *Idris* Förster (Hymenoptera: Scelionidae) is found to parasitize the eggs of *Bagrada hilaris* (Hemiptera: Pentatomidae) and is described as new: *Idris elba* Talamas, **sp. nov.** This is the first association of an *Idris* species with a non-spider host, and the association is confirmed with molecular diagnostic tools that enable identification of parasitoid and host from the remains of parasitized eggs.

Keywords

Bagrada bug, natural enemies, egg parasitoid, diagnostics

Introduction

The bagrada bug, *Bagrada hilaris* (Burmeister) (Hemiptera: Pentatomidae), is an invasive alien species that has recently established in North America (Palumbo et al. 2016) and is one of the most important pests of Brassicaceae worldwide because of the eco-

conomic damage it causes in many crops. This pest has 74 host species in 23 botanical families, but it prefers crops of the Brassicaceae family (Obopile et al. 2008, Palumbo 2016, Palumbo et al. 2016). The main damage to the plants is caused by direct feeding: the suction of sap causes a decrease in vigor and photosynthetic area. *Bagrada hilaris* is native to West Africa or Southeast Asia (Howard 1906, Perring et al. 2013, Palumbo et al. 2016) and is currently an important pest in India, Africa, southern Europe, southern Asia and the Middle East (Palumbo et al. 2016). In North America, it was first detected in Los Angeles, California, USA, in 2008, and by 2014 it had already spread to brassica crops in other locations in California and Arizona (Garrison 2009, Arakelian 2010, Palumbo et al. 2016). In Mexico it was first detected in 2014, in Saltillo, Coahuila (Sánchez-Peña 2014), and in 2017 reached the state of Guanajuato (Hernández-Chávez et al. 2018). Over 70% of Mexico's production of broccoli is in Guanajuato and it is the leading region for exports of broccoli and cauliflower to the USA and Canada, either as frozen or fresh products (SIAP 2018). More recently, this species was found in Santiago, Chile, in 2016 (Faúndez et al. 2016). The losses in California during 2013 were estimated at \$679 million USD (Palumbo 2016). Even though quarantine measures have been taken for this pest, its distribution appears to have reached important commercial crop regions in the Americas and it threatens to spread to more ecosystems with potential economic impact in cruciferous and other crops (Carvajal et al. 2018). To date, control measures for *B. hilaris* rely primarily on the use of pyrethroid, carbamate, and neonicotinoid insecticides (Sachan and Purwar 2007, Obopile et al. 2008, Joseph et al. 2016). However, biological control using native or exotic natural enemies might offer an alternative to maintain pest populations below the economic threshold.

Invasive species have the potential to serve as an abundant host resource for native natural enemies if they can recognize and exploit this new resource (Cornell and Hawkins 1993). However, new host-parasitoid associations can be difficult to conclusively identify at the species level using traditional rearing approaches and misidentifications or contaminated rearing can result in questionable linkages (Shaw 1994, Quicke 1997). When reliable reference sequences (e.g., DNA barcodes) are available, the incorporation of molecular forensic approaches that detect and identify trace amounts of host and parasitoid DNA can be used to validate host-parasitoid associations obtained using traditional approaches (Rougerie et al. 2011, Hrccek et al. 2011; Garipey et al. 2019). Several species of parasitoid wasp (primarily in the family Scelionidae) are known to attack *B. hilaris* eggs in India and Pakistan (Palumbo et al. 2016, Mahmood et al. 2015, Martel et al. 2019). To date, no native parasitoids have been reported to attack *B. hilaris* in the field in the USA, although the adventive *Trissolcus hyalinipennis* Rajmohana & Narendran and the intentionally introduced *Trissolcus basalis* (Wollaston) have been detected from sentinel egg masses of *B. hilaris* in California (Ganjisaffar et al. 2018). In Mexico, studies to define the natural enemy community that exploit this newly established pest have identified two native scelionid species parasitizing *B. hilaris* eggs: *Telenomus podisi* Ashmead and *Gryon myrmecophilum* (Ashmead) (Felipe-Victoriano et al. 2019). Unlike most stink bugs, which lay their eggs in large contiguous masses directly on a plant, *B. hilaris* mostly oviposits singly or in small groups of eggs (~10 eggs) in the soil, which may decrease the likelihood of ex-

ploitation by native, generalist stink bug egg parasitoids that typically forage for hosts on foliage (Reed et al. 2013). Prior to the consideration of exotic natural enemies for a classical biological control program for the bagrada bug, the native natural enemy community associated with this pest in the field must be investigated to determine if the native fauna can contribute toward a biological control solution. During the 2018 field season, a natural enemy survey was conducted in Guanajuato, México, to detect and identify native parasitoid species that can exploit this new host resource.

Scelionid egg parasitoids of *B. hiliaris* have been reported in natural field conditions from the native range of this species: *Gryon karnalensis* (Chacko and Katiyar 1961), *Telenomus samueli* (Mani and Sharma 1982), and *Psix* sp. (near *striaticiceps*) (Cheema et al. 1973). In this study, traditional rearing and taxonomic treatment of emerged parasitoid adults were employed in conjunction with molecular forensics to definitively link the trophic association between host species and parasitoid species based on trace amounts of DNA in emerged eggs. With the combination of these methods we show that another scelionid, *Idris elba* sp. nov., can also successfully parasitize eggs of *B. hiliaris* under natural field conditions.

Materials and methods

Field collections

Biweekly surveys were conducted between May and September 2018 in the municipalities of Abasolo and Juventino Rosas in Guanajuato, where large areas of broccoli, cauliflower and cabbage were planted. The sampling was conducted primarily in abandoned crops where insecticides were no longer used. In addition, crop edges where wild host plants (e.g., *B. campestris* L. and *B. nigra* (L.) W. D. J. Koch) of *B. hiliaris* occur were inspected. When a population of *B. hiliaris* was observed, the soil surrounding the plant was carefully inspected to collect the bug eggs. This material was separated from the substrate and placed in a Petri dish for transport to the laboratory.

Field-collected *B. hiliaris* eggs were kept in Petri dishes with a broccoli leaf in the laboratory in a bioclimatic chamber (26 ± 1 °C, $75 \pm 5\%$ RH and 12:12 (L:D) photoperiod). The material was checked daily to observe evidence of parasitism. Emerged parasitoids were placed in 1.5mL Eppendorf tubes with ethyl alcohol (70%); subsequently, they were processed and mounted. Empty eggs from which either nymphs or parasitoids emerged were placed (dry) in separate 1.5mL Eppendorf tubes for subsequent molecular forensic analysis.

Taxonomy

The description of *I. elba* was generated by the online systematics and taxonomy tool, vSysLab (vsyslab.osu.edu). Specimen records of *I. elba* and other species used in the comparative analysis are deposited in the Hymenoptera Online Database (hol.osu.edu).

Morphological terms largely follow Mikó et al. (2007) and were matched to concepts in the Hymenoptera Anatomy Ontology using the text analyzer function and a table of these terms and URI links is provided in Suppl. material 1.

Photography

Images of bagrada bug eggs and the wings of *I. elba* were produced with a Zeiss Stereo Discovery.V20, and images were captured with AxioCam IC-ZEN 2 lite software. Photographs of the lectotype of *I. howardi* were made available by Talamas et al. (2017). All other images of *I. elba* and *Idris* species for comparative illustration were taken with a Macroscopic Solutions Macropod Micro Kit with optical slices rendered in Helicon Focus.

Collections

Specimens used in this study are deposited in the following collections:

- CEAM** Colegio de Postgraduados Insect Collection, Texcoco, Estado de México, México
CNCI Canadian National Collection of Insects, Ottawa, ON, Canada
FSCA Florida State Collection of Arthropods, Gainesville, FL, USA
USNM National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

Abbreviations and characters annotated in the figures

- atc** acetabular carina (Figure 7)
eps episternal foveae (Figures 7, 10, 14)
lpa lateral propodeal area (Figures 16–19)
metd metasomal depression (Figures 16, 21)
mpit metapleural pit (Figure 6)
mpp mesopleural pit (Figure 7)
msct metascutellum (Figures 16–17)
nes netrion sulcus (Figures 8, 9, 13)
pcxs paracoxal sulcus (Figures 10, 11)
pdms posterodorsal metapleural sulcus (Figure 7)
prcs pronotal cervical sulcus (Figure 12)
pss pronotal suprahumeral sulcus (Figure 12)
sp2 anterior thoracic spiracle (Figure 13)
T1–T7 mediotergites 1–7 (Figures 20, 21)

Molecular analysis

Two parasitoid adult specimens that emerged from field-collected *B. hilaris* eggs were used as voucher material for DNA analysis to generate reference sequences. DNA from parasitoid adults was extracted non-destructively using a Chelex DNA extraction method (as described in Garipey et al. 2019) and amplified using universal COI barcode primers (LCO-1490 and HCO-2198; Folmer et al. 1994) following the protocol described by Hebert et al. (2003). In addition, DNA from emerged field-collected eggs was extracted and amplified following the protocol described by Garipey et al. (2019) for forensic analysis of empty stink bug eggs; eggs from which parasitoid adults (n=4) had emerged were processed using family-specific scelionid PCR primers (Scel-F1 and HCO-2198) (Garipey et al. 2019). Eggs from which stink bug nymphs had emerged (n=10) were processed with universal barcode primers (LCO-1490 and HCO-2198).

PCR products were visualized with a QIAxcel Advanced automated capillary electrophoresis system (Qiagen) using the DNA screening cartridge and method AL320. Results were scored with the Qiaxcel ScreenGel Software (version 1.2.0), and only samples of the expected fragment size with a signal strength exceeding 0.1 relative fluorescent units were scored as positive. Samples scored as positive were purified using ExoSAP-IT (Affymetrix, Santa Clara, California, USA) following the manufacturer's instructions. Purified PCR products were bidirectionally sequenced using the appropriate primers (SCEL-F1 and HCO-2198 for parasitized eggs or LCO-1490 and HCO-2198 for unparasitized eggs and parasitoid adults) on an ABI 3730 DNA Analyzer at the Robarts Research Institute (London Regional Genomics Centre, Ontario, Canada). Forward and reverse sequences were assembled and edited using CodonCode Aligner program, version 4.2.7 (CodonCode Corporation, Centerville Massachusetts, USA). Specimen data, assembled DNA sequences, and tracefiles for all samples that yielded sequences >400 bp were uploaded into BOLD under the project "Parasitoids of the genus *Idris* and their hosts" (IDRIS). DNA barcodes obtained from empty eggs were screened through the BOLD identification system to identify the host eggs based on publically-available DNA sequences in the identification engine. Parasitoid DNA obtained from the egg fragments was compared to the DNA barcode profiles generated from voucher *Idris* specimens for confirmation of species identity.

Results

A total of 88 *B. hilaris* eggs were collected across all sites surveyed in Guanajuato. Four parasitoids were recovered from 17 eggs collected May 31, 2018 (2 males, 2 females). These parasitoids emerged from eggs collected at the locality of Santa Cruz, municipality of Juventino Rosas, Guanajuato (20.622390N, 101.015655W). The parasitized eggs were collected in the soil near *Brassica nigra* plants, and the recovered species was

Table 1. Genbank Accession numbers for *Idris elba*.

Collecting Unit Identifier	Genbank Accession Number	Collection Locality
FSCA 00033237	MN135849	Santa Cruz, Guanajuato, Mexico
FSCA 00033238	MN135848	Santa Cruz, Guanajuato, Mexico
FSCA 00033127	MN135850	Sandoval County, New Mexico, USA

identified as a species in the genus *Idris* Förster (Hymenoptera: Scelionidae) based on the compact clava in females and other characters presented in Masner (1980).

DNA sequences were obtained for adult specimens and yielded a 649-bp COI fragment using the universal DNA barcode primers (LCO-1490, HCO-2198). Four out of 10 unparasitized stink bug eggs successfully amplified and sequenced using the universal COI barcode primers and were identified as *Bagrada hilaris* (100% identity) using the BOLD identification system (Genbank accession number MN135841–MN135844). The remaining unparasitized eggs yielded poor quality DNA sequences, likely due to insufficient or degraded DNA from unpreserved field-collected samples. Three out of the 4 parasitized eggs successfully amplified and sequenced using the scelionid PCR primers (Scel-F1, HCO-2198) (Genbank accession numbers MN135845–MN135847). The sequences were an exact match to the DNA barcode reference sequences obtained from the *I. elba* adults collected from the same site, thus corroborating the observational evidence that *I. elba* indeed emerged from field-collected *B. hilaris* eggs. COI sequences of these specimens and a specimen of *I. elba* from New Mexico have been uploaded to Genbank (Table 1).

Taxonomy

Idris elba Talamas, sp. nov.

<http://zoobank.org/26052F1D-C091-4398-9497-6689DC8AE0B7>

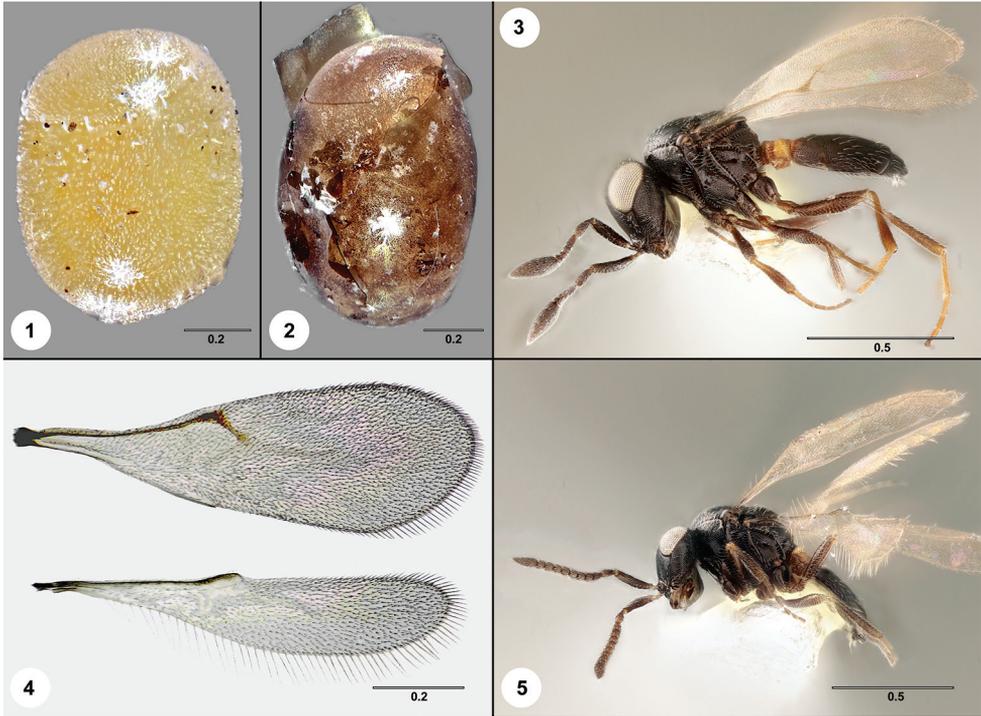
https://bioguid.osu.edu/xbiod_concepts/498223

Figures 3–5, 7, 9, 10, 16, 21

Description. Female body length: 0.85–1.16 mm (n=9). Male body length: 0.96–1.07 mm (n=2).

Head. Color of antenna: pale brown to black. Claval formula: 1-2-2-1. Mandible: tridentate, teeth of equal size. Number of clypeal setae: 6. Length of central keel: extending to midpoint of frons. Facial striae: short, not reaching ventral limit of compound eye. Malar striae: short and weakly indicated, not reaching ventral limit of compound eye. Hyperoccipital carina: present. Occipital carina: present ventrally, absent above midpoint of compound eye.

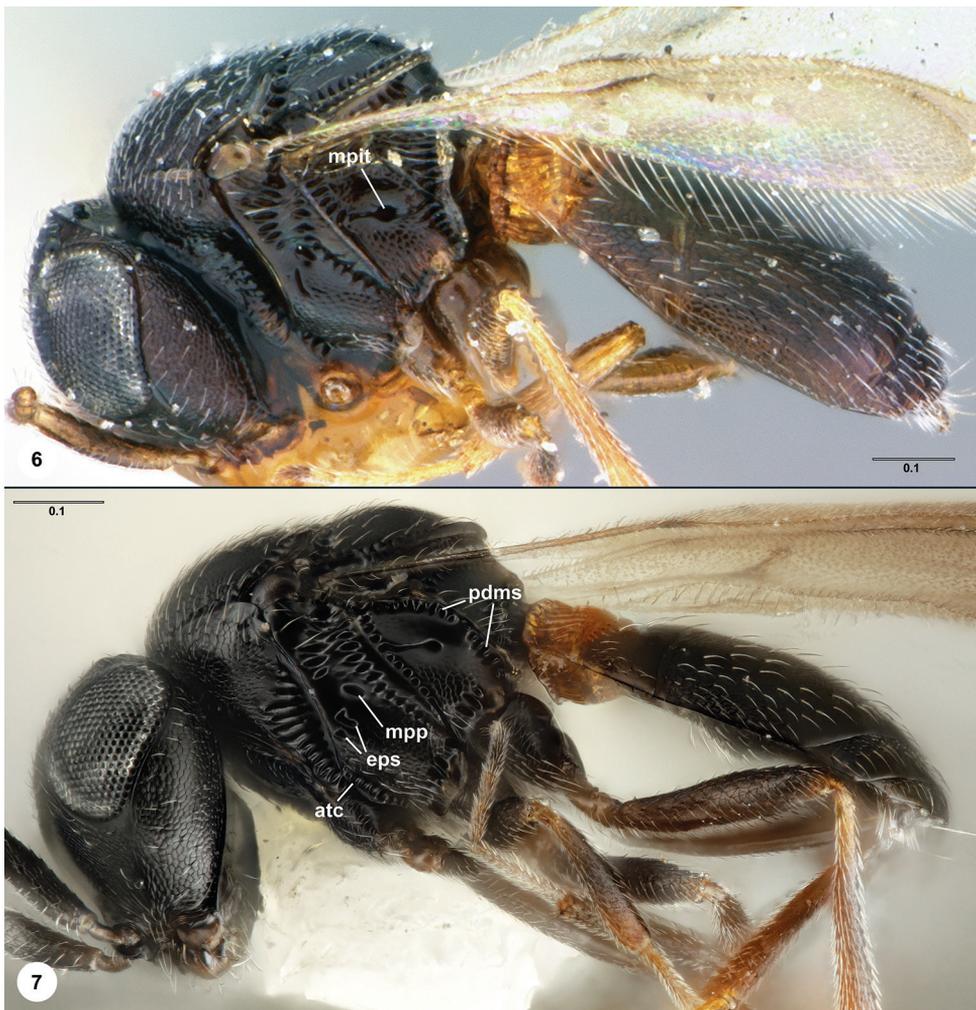
Mesosoma. Pronotal suprahumeral sulcus: absent. Epomial carina: absent. Pronotal cervical sulcus: absent. Dorsal terminus of netrion sulcus: ventral to anterior thoracic spiracle. Netrion sulcus: comprised of foveae, foveae elongate at midpoint of sulcus. Mesoscutal suprahumeral sulcus: foveate. Mesoscutal humeral sulcus: fove-



Figures 1–5. **1** unparasitized egg of *B. hilaris* **2** egg of *B. hilaris* from which *I. elba* emerged **3** *Idris elba*, holotype female (FSCA 00033238), lateral habitus **4** *Idris elba* paratype female (FSCA 00090587) fore and hind wings, dorsal view **5** *Idris elba*, paratype male (FSCA 00033237), lateral habitus. Scale bars: in millimeters.

ate. Scutoscutellar sulcus: smooth medially, foveate laterally in axillar area. Interior of axillar crescent: smooth. Posterior mesoscutellar sulcus: foveate, continuous around posterior and lateral margins of scutellar disc. Metanotal trough: foveate. Metascutellum: present as a smooth strip. Plical carina: absent. Lateral propodeal carinae: closely approximated medially. Perimeter of lateral propodeal area: foveate. Sculpture of lateral propodeal area: granulate; smooth. Sculpture of metasomal depression: radially striate; smooth. Propleural epicoxal sulcus: absent. Postacetabular sulcus: foveate. Mesopleural epicoxal sulcus: comprised of foveae. Intercoxal space: narrow, cells of postacetabular and mesopleural epicoxal sulci confluent ventrally. Number of episternal foveae: 2. Prespecular sulcus: present, not extending to mesopleural pit. Paracoxal sulcus in ventral half of metapleuron: foveate. Metapleural epicoxal sulcus: comprised of elongate foveae anteriorly, absent posteriorly. Metapleural sulcus: extending anteriorly from metapleural pit as a smooth furrow. Posterodorsal metapleural sulcus: foveate, interrupted medially.

Metasoma. Color of metasoma: T1–S1, anterior T2–S2 yellow to pale brown, otherwise brown to black. Horn on T1 in females: absent; Sculpture of T1: longitudinally striate. Sculpture of T2: weakly striate posterior to transverse sulcus. Sculpture of T3–T6: uniform coriaceous microsculpture. T6–T7: located ventral to T4–T5, not visible

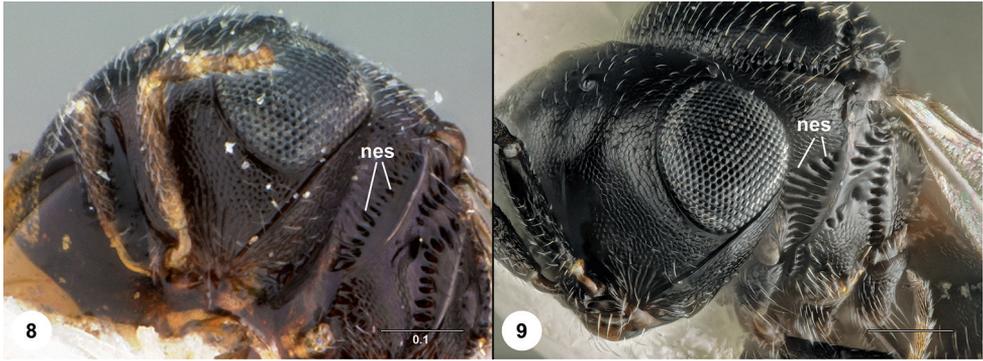


Figures 6, 7. *Idris howardi*, lectotype female (USNMMENT00989875), head, mesosoma, metasoma, lateral view **7** *Idris elba*, holotype female (FSCA 00033238), head, mesosoma, metasoma, lateral view. Scale bars: in millimeters.

in dorsal view. Sculpture of S1: longitudinally striate. Sculpture of S2: weakly striate posterior to transverse sulcus. Sculpture of S3–S6: uniform coriaceous microsculpture.

Variation. We observed notable variation in the degree of development of two characters. The microsculpture of the lateral propodeal area can be distinctly granulate (Figures 10, 21) or mostly smooth (Figure 16), and sculpture of the metasomal depression varies from radially striate (Figure 21) to mostly smooth (Figure 16)

Material examined. Holotype, female: **MEXICO**: 20.622390N, 101.015655W, Santa Cruz de Juventino Rosas, Guanajuato, 18.V.2018, reared from *Bagrada hilaris* egg, FSCA 00033238 (deposited in FSCA). Paratypes: (9 females, 3 males) **MEXICO**: 1 female, 2 males, FSCA 00090587–00090588 (CEAM); FSCA 00033237 (FSCA).

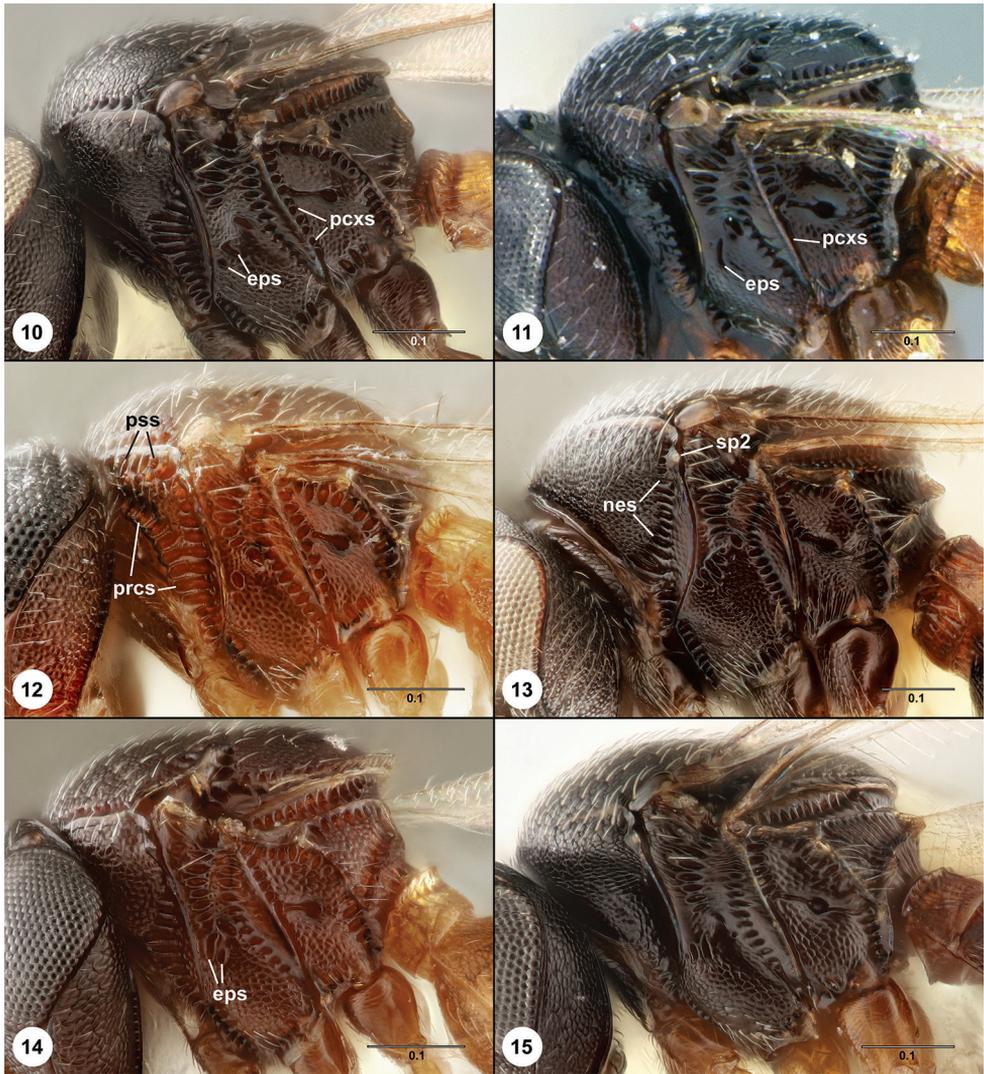


Figures 8, 9. **8** *Idris howardi*, lectotype female (USNMENT00989875), head and mesosoma, anterolateral view **9** *Idris elba*, holotype female (FSCA 00033238), head and mesosoma, anterolateral view. Scale bars: in millimeters.

UNITED STATES: 8 females, 1 male, FSCA 00090463 (CNCI); FSCA 00033127 (FSCA); USNMENT01335975–01335981 (USNM).

Diagnosis. It should be noted that our diagnosis is presented without full knowledge of the diversity of Nearctic *Idris* and additional comparison to the images, description, and sequence data here provided may be necessary to confirm the species identity. From the material that we have examined, *Idris elba* can be identified by the combination of the following characters: netrion sulcus complete and dorsally terminating ventral to the anterior thoracic spiracle; pronotal suprahumeral sulcus absent; pronotal cervical sulcus absent; episternal foveae arranged along a line between the mesopleural pit and the dorsal apex of the acetabular carina; paracoxal sulcus comprised mostly or entirely of foveae in the ventral half of the metapleuron; metapleural sulcus absent posterior to the metapleural pit; lateral propodeal area without rugae or longitudinal striation; T1 in females without horn; T6–T7 located ventral to T4–T5.

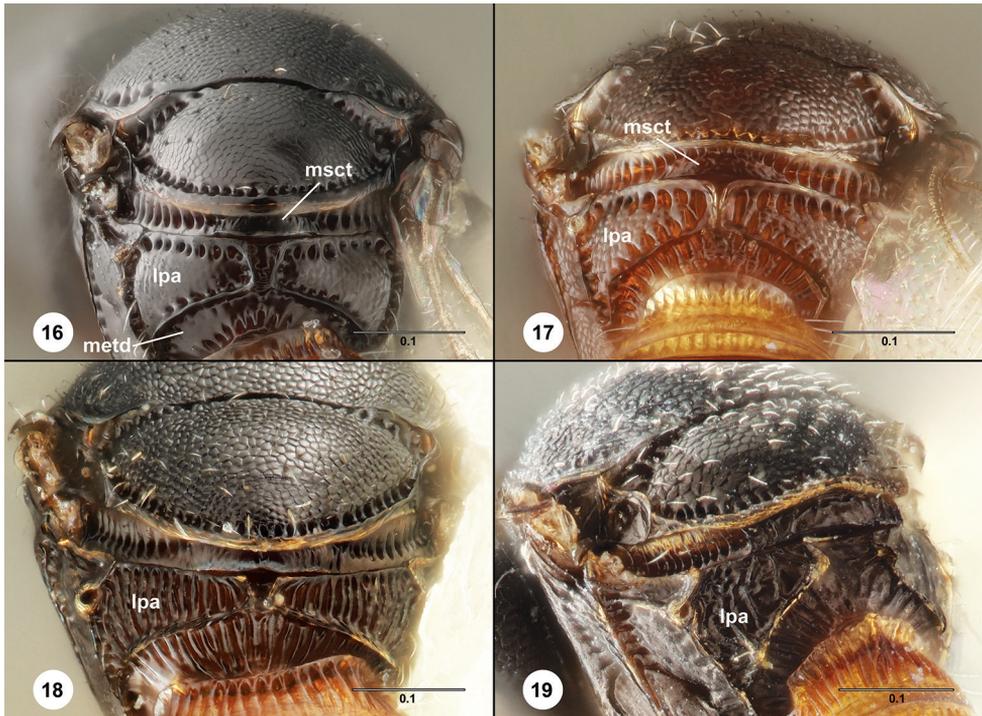
Two distinct characters are found in *I. elba* and numerous other species of Nearctic *Idris*, the color pattern of a dark body with a distinctly lighter T1/S1 and anterior T2/S2 (Figures 3, 5–7, 20, 21), and the form of the metasoma in which T6–T7 are oriented vertically and are largely obscured from dorsal view (Figures 20, 21). Among the described species of the Nearctic region, *I. howardi* is morphologically closest to *I. elba* and exhibits both traits. *Idris howardi* can be separated by the striate lateral propodeal area (Figure 20), the ventral portion of the paracoxal sulcus expressed as a simple furrow (Figure 11), and the small size of foveae of the netrion sulcus (compare Figures 8, 9). The absence of rugae or striae in the lateral propodeal area is very useful for diagnosing *I. elba* (compare Figures 10–19) but can be found in at least one other species from the region. This species can be separated by the paracoxal sulcus taking the form of a smooth furrow in the ventral half of the metapleuron, the episternal foveae arranged perpendicular to a line between the mesopleural pit and the dorsal apex of the acetabular sulcus (Figure 14) and the foveae of the metanotal trough forming a con-



Figures 10–15. **10** *Idris elba*, holotype female (FSCA 00033238), mesosoma, lateral view **11** *Idris howardi*, lectotype female (USNMENT00989875), mesosoma, lateral view **12** *Idris* sp., female (FSCA 00090464), mesosoma, lateral view **13** *Idris* sp., female (FSCA 00033145), mesosoma, lateral view **14** *Idris* sp., female (FSCA 00090465), mesosoma, lateral view **15** *Idris* sp., male (FSCA 00090467), mesosoma, lateral view. Scale bars: in millimeters.

tinuous line above the metascutellum (Figure 17). In female specimens of *I. elba*, the metascutellum interrupts the line of foveae across the metanotal trough (Figure 16).

We encountered one other species with the ventral portion of the paracoxal sulcus comprised of cells (Figure 12), and this species can easily be separated by the presence of distinct pronotal cervical and pronotal suprahumeral sulci on the lateral pronotum (Figure 12). We emphasize the utility of mesosomal sulci for future taxonomic studies, which exhibit an exceptional diversity of form in *Idris*. One remarkable species from

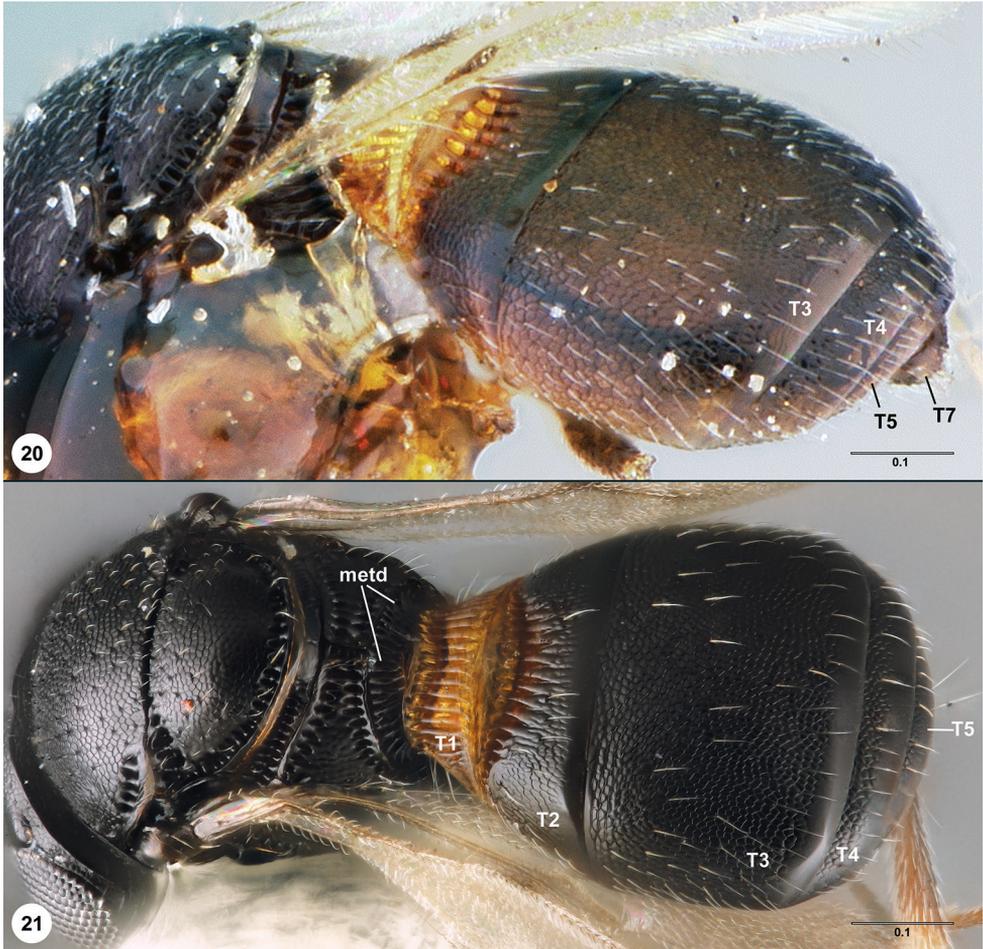


Figures 16–19. **16** *Idris elba*, paratype female (FSCA 00090463), mesosoma, posterolateral view **17** *Idris* sp., female (FSCA 00090465), mesosoma, posterolateral view **18** *Idris* sp., male (FSCA 00090467), mesosoma, posterolateral view **19** *Idris* sp., (FSCA 00090466), mesosoma, posterolateral view. Scale bars: in millimeters.

the mid-Atlantic USA features a netrion sulcus that terminates *anterior* to the anterior thoracic spiracle (Figure 13). Within Platygastroidea this unusual form is known to us only from *Nixonia* Masner (Nixonidae) (Mikó et al. 2007).

Etymology. The epithet “*elba*” is an arbitrary combination of letters that is to be treated as a noun in apposition.

Comments. It is our opinion that the description of a new species from a genus as large and unexplored as *Idris* outside of the context of a thorough revision generally should be avoided. In the case of *Idris elba*, we justify our treatment based on the following: First, we are confident that *I. elba* has not been described previously from the Nearctic region. *Idris elba* clearly does not belong to the *I. melleus* species group treated by Masner and Denis (1996) based on the characters they presented, including “head moderately to remarkably large relative to the mesosoma and metasoma”, and “propodeum canaliculate (except in *I. pulvinus*)”. Images of all other species from the Nearctic are available via the online image database *Specimage* (specimage.osu.edu), provided by Norman Johnson (The Ohio State University) and Talamas et al. (2017). Based on these images, *Idris elba* can be separated from all described Nearctic species outside of the *melleus* group by the smooth lateral propodeal area, foveate mesoscutal humeral sulcus, and T6–T7 located ventral to T4–T5. Second, we considered the possibility



Figures 20, 21. **20** *Idris howardi*, lectotype female (USNMENT00989875), mesosoma and metasoma, dorsolateral view **21** *Idris elba*, holotype female (FSCA 00033238), mesosoma and metasoma, dorsal view. Scale bars: in millimeters.

that *I. elba* is an adventive species, given that the phenomenon of adventive populations of parasitoids following their invasive hosts is now well documented and has occurred with bagrada bug in North America (Ganjisaffar et al. 2018). We contend that this is highly unlikely because some specimens of *I. elba* were collected in New Mexico in 2008 (Sandoval Co.), two years prior to the first detection of *B. hilaris* in this state (Doña Ana Co.) (Bundy et al. 2012). Last, the host association of *Idris* with bagrada bug eggs is of agricultural consequence with implications for the ability of parasitoids to shift between phylogenetically distant hosts (Araneae and Hemiptera), and thus there is an immediate need to formally refer to this species. Revising the species of Nearctic *Idris* is a project requiring years of work and for which resources are not currently available. This situation exemplifies the need for a pre-existing taxonomic framework for parasitoid Hymenoptera, including taxa where the economic importance is not obvious. To that end, this publication may provide impetus for taxonomic revision of Nearctic *Idris*.

Discussion

Most hymenopteran parasitoids attack a narrow range of closely related host species, resulting from the coevolutionary arms race that restricts the ability of a parasitoid to develop in novel, phylogenetically distant host species (Godfray 1994, Rossinelli and Bacher 2014). However, there are some exceptions. For example, egg parasitoids belonging to the genus *Anastatus* Motschulsky (Hymenoptera: Eupelmidae) can often attack and develop in insects from different orders, and some can develop in eggs of pentatomids, mantids, and various Lepidoptera (Rao et al. 1971, Fritz et al. 1986, Jones 1988). The host range of a parasitoid is of considerable interest from ecological and evolutionary perspectives but is often difficult to interpret due to misidentifications of parasitoid and host species, contaminated rearing (Shaw 1994, Quicke 1997), and the logistical challenges of locating small, cryptically located hosts (eggs) in the environment. To overcome these difficulties, we used traditional rearing and a molecular forensic approach to detect and identify trace amounts of DNA to confirm the host-parasitoid associations in field-collected host eggs.

Members of the genus *Idris* are known to be solitary, primary parasitoids of spider eggs (Hickman 1967, Austin 1981, Masner and Denis 1996) and have not been reported previously from other arthropod hosts. *Idris* species are known from a variety of spider families and are thought to have a high degree of host group specificity (Iqbal and Austin 2000). However, there are no data available on the degree of host specificity within individual wasp species, and to date no egg parasitoids from the tribe Baeini (including *Idris*) have been reared from a host other than a spider (Johnson et al. 2018). The discovery of *I. elba* as a parasitoid of *B. hiliaris* is thus quite unexpected and suggests the potential for a much broader host range of *Idris* – one that includes both spider and insect hosts. The distinctive oviposition behavior of *B. hiliaris*, wherein eggs are laid in the soil (as opposed to on the plant like most pentatomids), suggests the possibility that the host selection and specificity of *Idris* may be based on habitat overlap between *B. hiliaris* eggs and spider eggs. As suggested by Strand and Obrycki (1996), shared ecology can be used to predict the host range of a natural enemy, where a parasitoid will attack a diversity of arthropods occurring in a defined habitat. This may be a case of accidental parasitism by *I. elba*, based on chance encounters with *B. hiliaris* eggs in the same habitat as its typical spider host. The physiological and developmental suitability of *B. hiliaris* eggs for *I. elba* is remarkable given the fact that the accidental host is not closely related to the hosts that are usually attacked by *Idris* species. Although largely speculative, it is possible that some of the strategies used to overcome host defenses are conserved within Scelionidae and confer some level of developmental success in a non-target host. To some extent this must be the case as numerous host shifts have occurred in the family (Austin et al. 2005). The degree of parasitism that *I. elba* can achieve on *B. hiliaris* is unknown, and further investigation on the frequency of occurrence, developmental success, and potential fitness consequences associated with development in *B. hiliaris* merits investigation, not only to determine its potential contribution to biological control strategies for this pest in Mexico, but also to provide improved understanding of this unlikely host-parasitoid association. The synergy of carefully executed field studies, traditional taxonomy and molecular forensics to identify the occurrence of *I. elba* in *B. hiliaris* shows the value of complementary methods in

the discovery of host-parasitoid associations and provides strong supporting evidence for associations that might otherwise be considered unlikely to occur in nature.

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Supplementary material I

URI table of HAO morphological terms

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Data type: species data

Explanation note: This table lists the morphological terms used in this publication and their associated concepts in the Hymenoptera Anatomy Ontology.

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