

Monotypic no more – a new species of the unusual genus *Schwarzia* (Hymenoptera, Apidae, Biastini)

Silas Bossert^{1,2}

1 Department of Entomology, Cornell University, Ithaca, New York 14853, USA **2** Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA

Corresponding author: Silas Bossert (sb2346@cornell.edu)

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Abstract

Schwarzia elizabethae Bossert, **sp. n.**, a previously unknown species of the enigmatic cleptoparasitic genus *Schwarzia* Eardley, 2009 is described. Both sexes are illustrated and compared to the type species of the genus, *Schwarzia emmae* Eardley, 2009. The male habitus of *S. emmae* is illustrated and potential hosts of *Schwarzia* are discussed. Unusual morphological features of *Schwarzia* are examined in light of the presumably close phylogenetic relationship to other Biastini. The new species represents the second species of Biastini outside the Holarctic region.

Keywords

Bees, cleptoparasitism, East Africa

Introduction

Biastini (Apidae, Nomadinae) is a small tribe of cleptoparasitic bees with just 13 described species in four genera (Ascher and Pickering 2019). Their distribution is primarily Holarctic. *Biastes* Panzer, 1806 is Palearctic and has five described species. Four species were treated by Warncke (1982), and *B. popovi* Proshchalykin & Lelej, 2004 has been described since. *Neopasites* Ashmead, 1898 has five described species restricted to the Nearctic; they are morphologically similar to *Biastes* and the genera were synonymized by certain authors (e.g., Warncke 1982). Currently, *Neopasites* is regarded

as a separate genus (Michener 2007). The distinguishing morphological characters are rather unobtrusive, but unambiguous and stable over their entire distribution. The only other Nearctic biastine genus is *Rhopalolemma* Roig-Alsina, 1991, with two described species and a morphology that is somewhat different than the remaining Biastini (Roig-Alsina 1991, Rozen et al. 1997). For example, *Rhopalolemma* lacks the preapical mandibular tooth that all other Biastini have (Michener 2007; but see discussion below) and the number of submarginal cells may be more variable. While all other Biastini have two submarginal cells (of varying length), individuals of *Rhopalolemma* were documented with 2 or 3 cells, sometimes in the same individual (Rozen et al. 1997). However, intraspecific variation in the number of submarginal cells is not uncommon in bees, and bees that have principally two submarginal cells are more likely to gain a third cell rather than losing the second cell (Scarpulla 2018).

The fourth genus and the most recently described biastine bee was *Schwarzia emmae* Eardley, 2009. It is an enigmatic bee with bizarre morphological characters that required the description of a new genus. Eardley (2009) assigned *Schwarzia* to Biastini based on shared morphological features with *Biastes*, i.e., the presence of a pre-apical mandibular tooth, the number of two submarginal cells (of different lengths), and the elevated median area of the metanotum (Eardley 2009). He further highlighted the striking morphological differences. Most notably, the disc of the fifth tergum of the female is strongly modified with a pre-apical pseudopygidial plate (Eardley 2009), which contrasts the surrounding area with its smooth surface, ivory-colored integument, and anterior brush of thick setae (see below). Additionally, tergum 5 extends posteriorly with two arched projections, forming an opening which is somewhat hourglass-shaped. The sixth sternum (illustrated in Eardley 2009, van Noort 2019) is spinose, slightly hooked posteriorly, and protrudes through the opening of the fifth tergum. Such modifications are unique among bees, and an adaptive function is not understood. However, modifications of terminal metasomal segments are very common in Nomadinae, particularly of the sixth sternum (Roig-Alsina 1991, Michener 2007). They presumably serve specific functions during oviposition of the parasites' eggs into the host bees' brood cells (Roig-Alsina 1991, Torchio 1986). Rare detail is provided by Torchio and Burdick (1988), who describe how the cleptoparasite *Epeolus compactus* Cresson, 1878 uses the spinose sixth sternum to slice openings into the lining of the host's brood cell. Unfortunately, no observational data which could elucidate the significance of the modified terminal structures of female *Schwarzia* is available, and potential host(s) are unknown.

Up to now, *Schwarzia* was only known from the type species and from very few records. All localities are in Eastern Africa, thereby rendering the genus the only Biastini outside the Holarctic (Eardley 2009). During a survey of Malaise trap material from Kenya, donated to the Smithsonian National Museum of Natural History by Robert S. Copeland, a second undescribed species was found, along with new records of *S. emmae*. The aim of this study is to describe the new species and provide new insights on the classification and morphology of the genus. I further discuss potential hosts in light of other bees collected during the same collecting events.

Material and methods

Specimens were collected in Kenya during four collecting events in 1998 and 1999. The type locality of the newly described species is in Tsavo East National Park in eastern Kenya, which is dominated by xeric plains and savanna habitats. As all specimens were collected in Malaise traps, no information on flower visitation is available. Photographs were taken with a Macropod Pro imaging system, consisting of a Canon EOS 6D camera and a Stackshot 3× Cognisys device. Z-stacking was carried out with Zerene Stacker Pro stacking software v1.04. The distribution map was generated with SIMPLMAPPR (Shorthouse 2010).

The holotype is deposited in the type collection of the National Museums of Kenya (NMK). All but one paratype are deposited in the collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). A male paratype is kept in the Packer Collection at York University, Canada.

The following abbreviations are used in the description: tergum (T), sternum (S), flagellomere (FL). For the description of the male, morphometric measures are given as a range from the smallest to the largest specimen examined.

Taxonomy

Schwarzia elizabethae Bossert, sp. n.

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Figs 1–4

Material examined. KENYA: Eastern Province, at Athi River, Tsavo East National Park, 2°38.51'S, 38°21.98'E, 22.–29.XI.1999, leg. R. Copeland, Malaise trap, 5♂, 1♀. Eastern Province, at Athi River, Tsavo East National Park, 2°38.51'S, 38°21.98'E, 29.III–1.IV.1999, leg. R. Copeland, Malaise trap, 1♂.

Diagnosis. Forewing with two submarginal cells, first of which at least twice as long as second (Fig. 1A). Omaulus lamellate. Labrum broader than long. Body size smaller compared to *S. emmae* (*S. elizabethae*: 5.1–5.9 mm, *S. emmae*: 6.3–8.8 mm). Protrusions on supra-antennal area absent (present in *S. emmae*), area evenly punctate (Figs 2C, 4C). Margin of compound eye entire, not indented as in *S. emmae* (Figs 2C, 4C). Punctuation on T1–T4 dense and distinctly coarser compared to *S. emmae* (Figs 2A–B, 4A–B). Integument color of tegulae tawny (compared to dark brown in *S. emmae*; Fig. 2G–H). Distinct pre-apical mandible tooth absent. Integument color of legs largely brown. Male: FL2–FL4 at least two times broader than long (Fig. 2E). Female: S5 in lateral view evenly rounded, median area shiny, without punctuation (S5 in lateral view more angled and with punctuation in *S. emmae*; Fig. 4E–F).

Description. Male (Fig. 1). Head: Head (Fig. 1B) wider than long (1.6–1.9 mm width to 1.2–1.4 mm length). Integument black with thick short setae around antennal sockets, clypeus, labrum, genal area, vertex. Antennal sockets in lower half of frons.

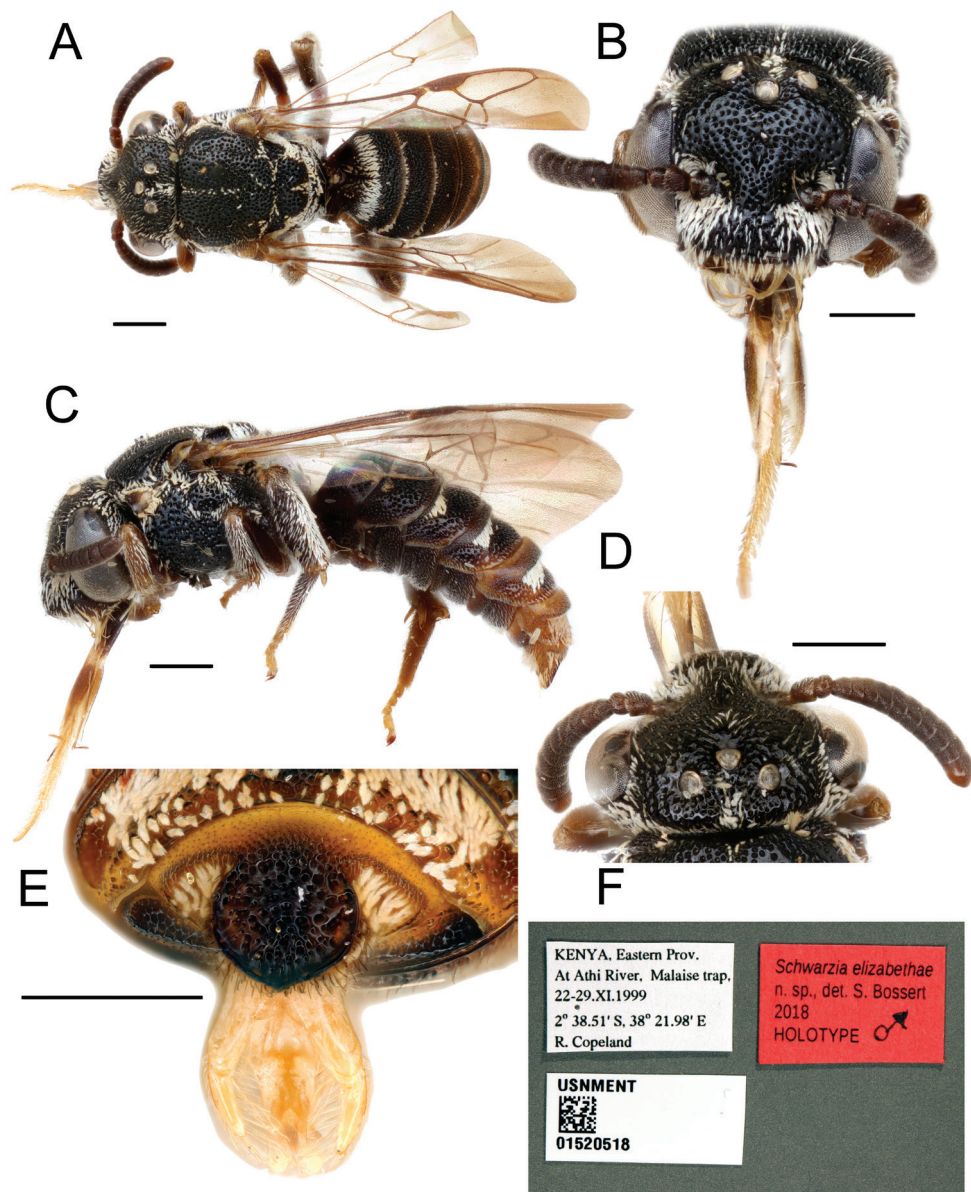


Figure 1. *Schwarzia elizabethae* Bossert, sp. n., holotype, male **A** habitus, dorsal view **B** head, frontal view **C** habitus, lateral view **D** head, dorsal view **E** tergum 7 with pygidial plate and genital capsule **F** label information as deposited with the holotype. Scale bars: 0.5 mm.

Clypeus protruding, much shorter than broad (0.6–0.8 mm width to 0.2–0.3 mm length). Punctuation on clypeus deep and coarse. Interspaces shiny, averaging less than half diameter of individual pits. Mandible dark, densely hairy, pre-apical teeth absent or just very minutely produced, outer ridge strongly developed. Labrum broad, about

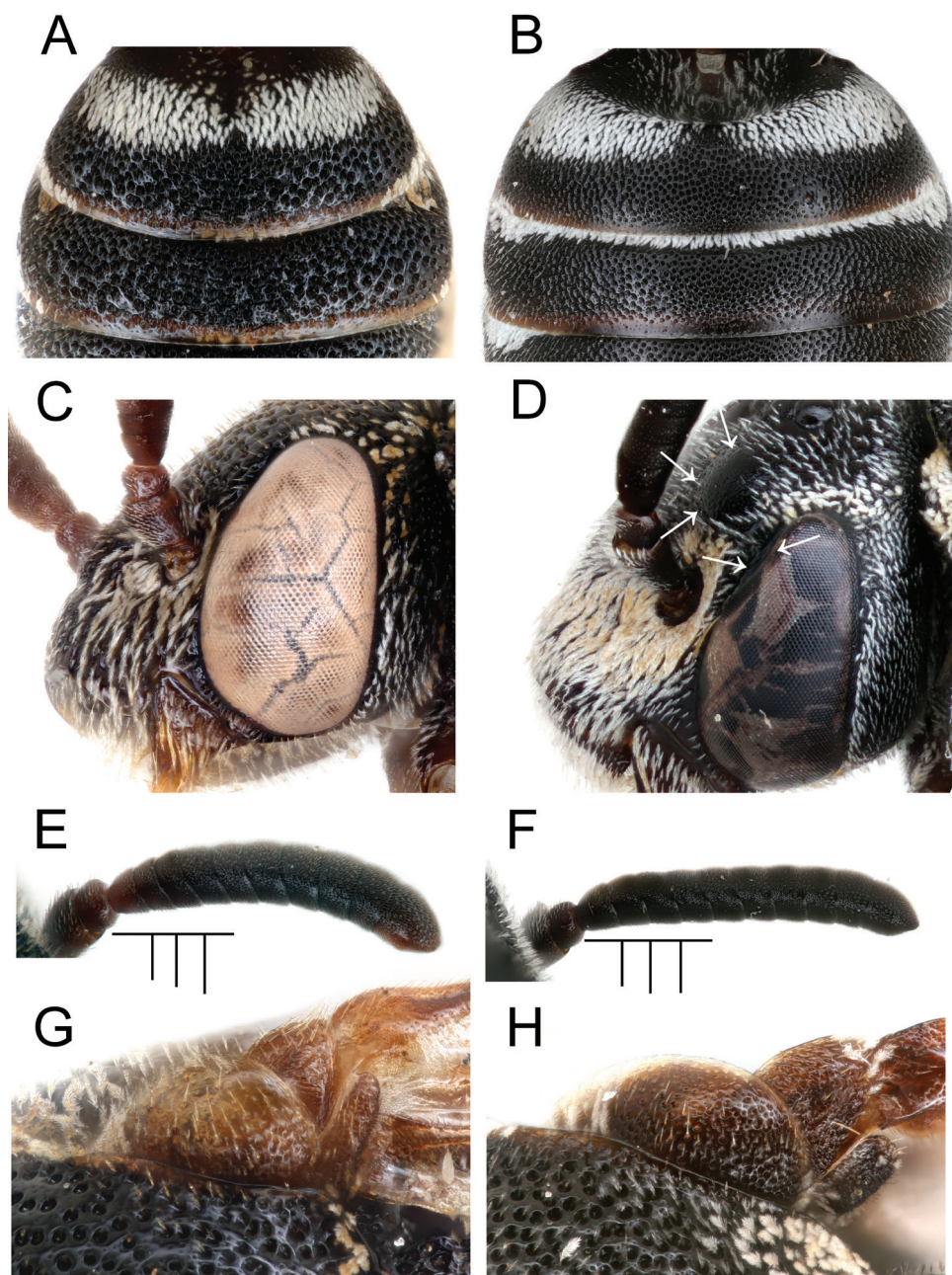


Figure 2. Comparison of selected diagnostic characteristics of males of *Schwarzia elizabethae* Bossert, sp. n. (left column: **A, C, E, G**) vs. *S. emmae* Eardley, 2009 (right column: **B, D, F, H**) **A–B** discs of T1 and T2 **C–D** head characteristics in lateral view. Arrows point to finely pitted protrusions on frontal area of *S. emmae* and to the intended inner margin of the compound eye **E–F** antennae **G–H** tegulae.

1.3× times broader than long. Proboscis very long (~2.5–2.8 mm, Fig. 1A–C). Maxillary palps with 2 palpomeres, labial palps with 3. Width of compound eye exceeds twice genal width in lateral view (Figs 1C, 3C). Deep, pit-like punctation more or less evenly distributed on supraclypeal area, supra-antennal area, frons, vertex (Fig. 1B, 1D). Interspaces shiny. Flagellum with 10 flagellomeres, FL2 (0.14–0.18 mm width to 0.07–0.08 mm length) and FL3 (0.16–0.19 mm width to 0.07–0.08 mm length) at least twice as broader as long (Fig. 2E). Coloration black to brown. Diameter of lateral ocellus 0.13–0.14 mm, median ocellus 0.14–0.15 mm. Ocellocular distance 0.32–0.35 mm. Mesosoma: Integument black, except legs and pronotal lobe tawny-colored (Fig. 1A–C). Short-thick setae primarily present on margins of segments, i.e., along episternal groove, scrobal groove, around pronotal lobe, posterior margin of scutum, around scutellum, along midline of scutum, on metanotum and metapostnotum. Intertergular distance 1.2–1.5 mm. Axillae weakly produced. Size and density of punctation on scutum similar to punctation on vertex. Interspaces shiny, up to 3 times puncture diameter. Punctation on scutellum slightly larger and denser. Integument of tegulae largely light-colored (Fig. 2G). Wing venation brown. Meso- and metatibial spurs with two ventrally oriented rows of teeth, most strongly produced on metatibia. Metasoma: Integument predominantly black. Junctions of terga brown. T1 with basal patch of thick white setae. T1–T5 with basal bands of setae, which may be covered by apical margin of preceding tergum. Punctation on T1–T5 coarse, interspaces smaller than pit diameters (Fig. 2A). T6 covered with setae. T7 with distinctly pitted pygidial plate, shown together with genital capsule in Fig. 1E. S5 with single patch of white setae medially. Remaining visible sterna unmodified.

Female (Fig. 3). Overall very similar to male except terminal terga. Head: Head (Fig. 3B) wider than long (1.8 mm width to 1.4 mm length). Integument black with thick short setae around antennal sockets, clypeus, labrum, genal area, vertex. Antennal sockets in lower half of face. Clypeus protruding, much shorter than broad (0.8 mm width to 0.3 mm length). Punctation on clypeus deep, more irregular than on supra-antennal area and frons. Interspaces shiny, averaging less than half diameter of individual pits. Mandible mostly brown, tips darkened. Mandible densely hairy, pre-apical teeth absent, outer ridge strongly developed. Labrum broad, about 1.3× times broader than long. Maxillary palps with 2 palpomeres, labial palps with 3. Width of compound eye exceeds twice genal width in lateral view (Figs 3C, 4C). Deep, pit-like punctation evenly distributed on supraclypeal area, supra-antennal area, frons, vertex (Fig. 3B, 3D). Protrusions on frontal area entirely absent. Flagellum with 10 flagellomeres, FL2 (0.14–0.18 mm width to 0.07–0.08 mm length) and FL3 more than twice as broad as long. Coloration black to brown. Diameter of lateral ocellus 0.14 mm, median ocellus 0.16 mm. Ocellocular distance 0.36 mm. Mesosoma: As in male except intertergular distance 1.4 mm. Metasoma: Integument predominantly black. T3–T4 laterally brown. T5 laterally and apically brown. T1 with basal patch of thick white setae. Punctation on T1–T4 coarse, interspaces generally smaller than pit diameters (Fig. 4A). Disc of T5 (Fig. 3E) bears distinct teardrop-shaped, ivory-colored pseudopygidial plate with anterior brush of golden setae. Posterior T5 with

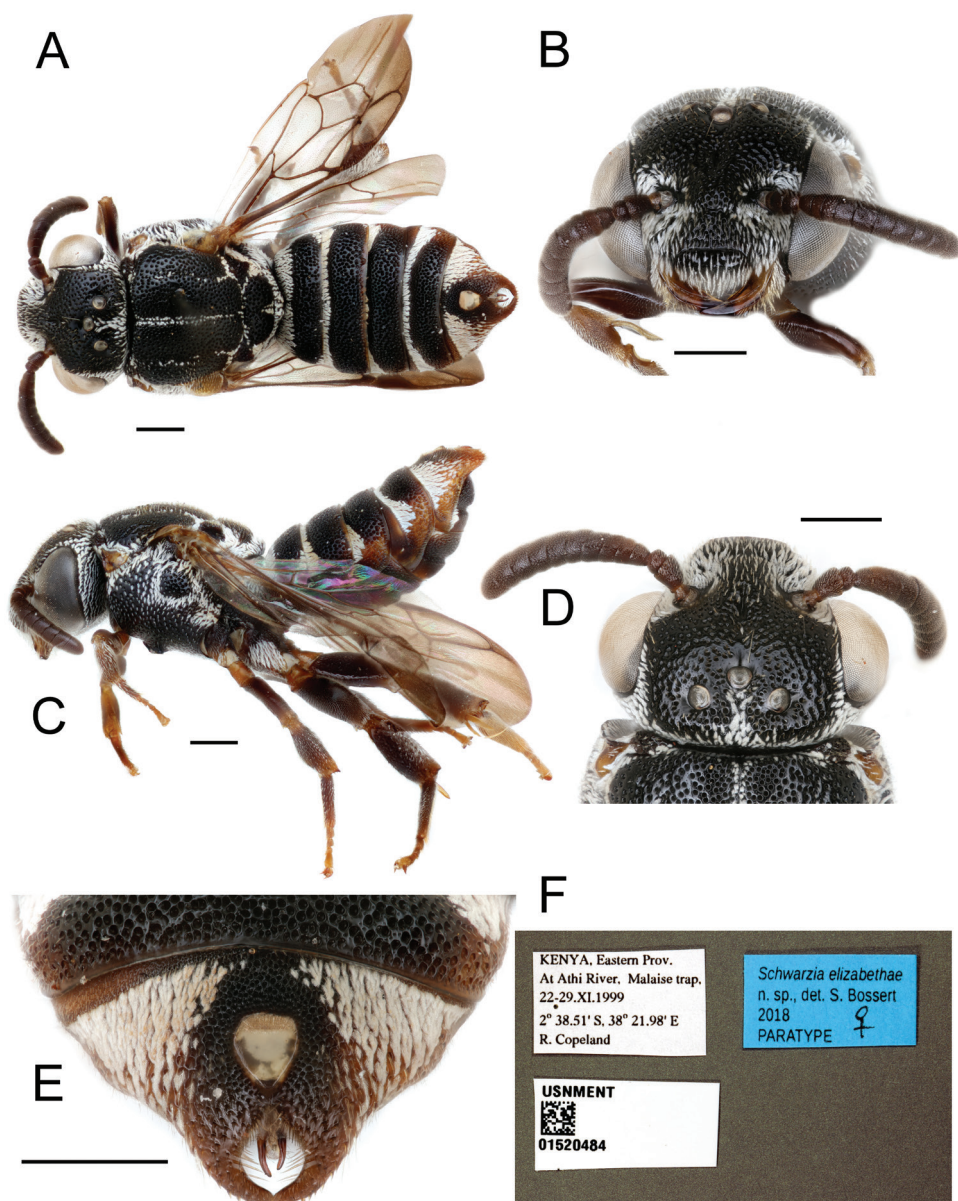


Figure 3. *Schwarzia elizabethae* Bossert, sp. n., paratype, female **A** habitus, dorsal view **B** head, frontal view **C** habitus, lateral view **D** head, dorsal view **E** tergum 5 **F** label information as deposited with the only female paratype. Scale bars: 0.5 mm.

two hook-shaped projections medio-laterally, forming opening through which bifid S6 protrudes. Punctuation on basal areas of S2–S5 fine and granulose, distinctly different from coarser punctuation medially and posteriorly. S1–S5 without median patches of setae.

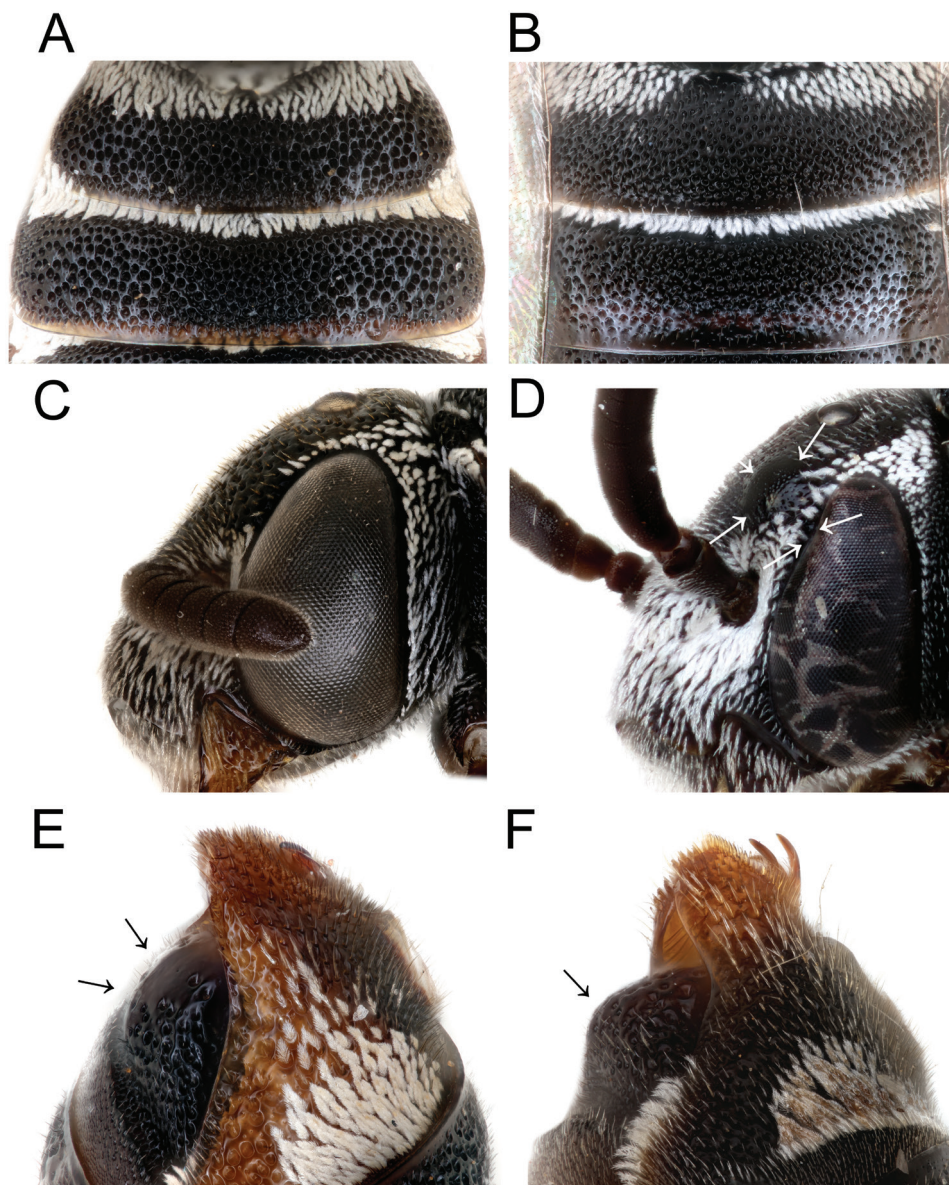


Figure 4. Comparison of selected diagnostic characteristics of females of *Schwarzia elizabethae* Bossert, sp. n. (left column: **A, C, E**) vs. *S. emmae* Eardley, 2009 (right column: **B, D, F**) **A–B** discs of T1 and T2 **C–D** head characteristics in lateral view. Arrows point to finely pitted protrusions on frontal area of *S. emmae* and to the intended inner margin of the compound eye **E–F** details of T5. Arrows point to the differently curved median area of the disc.

Etymology. Males of both described species of *Schwarzia* have only 10 flagellomeres. For nearly all species of bees, male individuals have 11 flagellomeres and females have 10 (Michener 2007, Schmiedeknecht 1930). As both sexes of *Schwarzia* have this character, which is usually associated with females, it seems appropriate to designate fe-

male first names as species names for the genus. The first described species of the genus, *Schwarzia emmae*, was named after Emma Schwarz, the late wife of Austrian melittologist Maximilian Schwarz (Eardley 2009). The new species is named after American hymenopterist Elizabeth A. Murray.

Additional records. KENYA: Eastern Province, base of Ukasi Hill, 0°49.262'S, 38°32.666'E, 21.XI.-05.XII.2011, leg. R. Copeland, Malaise trap, *Acacia/Commiphora* savanna, 1♀. Eastern Province, base of Ukasi Hill, 0°49.201'S, 38°32.627'E, 5.-12.V.2018, leg. R. Copeland, Malaise trap, *Acacia/Commiphora* savanna, 1♂. Eastern Province, Mulu Musingila farm, 2°6.847'S, 38°14.393'E, 13.-27.XII.2016, leg. R. Copeland, Malaise trap, farmland near small seasonal wet area, 1♂. All additional records are deposited in the ICIPE collection, Nairobi, Kenya.

Distribution. The species is known from four different localities, all of which are in the former Eastern Province of Kenya (Fig. 5). All sites are dominated by savanna type habitats.



Figure 5. Distribution map of *Schwarzia*, including the reported localities from Eardley (2009). Shown are selected towns near the collection localities.

***Schwarzia emmae* Eardley, 2009**

Figs 2, 4, 6, 7

Material examined. KENYA: Rift Valley Province, Mathews Range, Sarara Camp, 1.1°N, 37.387°E, 10.-13.VI.1998, leg. R. Copeland, Malaise trap, 1♂, 1♀, dep. in USNM. Eastern Province, near Athi River, Tsavo East National Park, 2°37'S, 38°22'E, 10.VI.1998, leg. R. Copeland, Malaise trap, 1♂, 1♀, dep. in USNM.

Distribution. With two newly reported collecting sites, the species is now known from a total of five different localities in Kenya and Tanzania (Fig. 5).

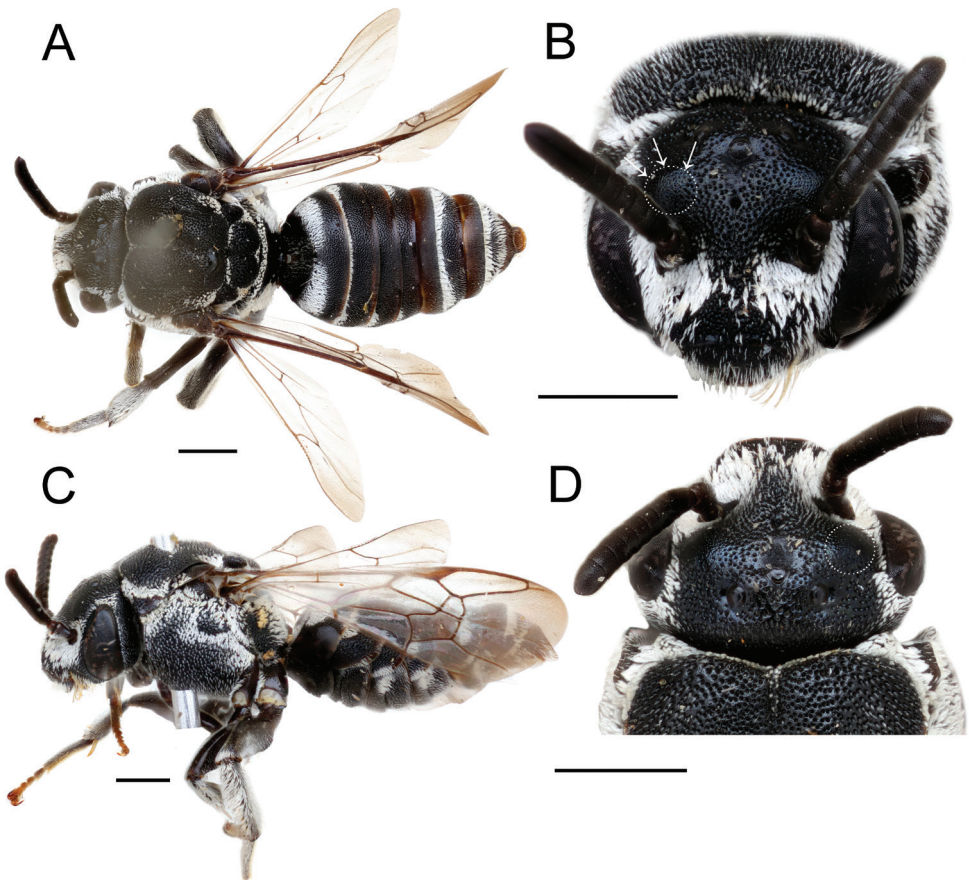


Figure 6. *Schwarzia emmae* Eardley, 2009, male **A** habitus, dorsal view **B** head, frontal view. Dotted line highlights the paired protrusions on the frontal area, which are noticeably more finely pitted than the surround areas **C** habitus, lateral view **D** head, dorsal view. Scale bars: 1 mm.



Figure 7. Comparison of modified apical terga of different female Biastini **A** *Biastes brevicornis* **B** *Neopasites fulviventrtris* **C** *Schwarzia emmae*. Scale bars: 1 mm.

Discussion

Classification and morphological features

Schwarzia are unusual bees that can easily be recognized and distinguished from other cleptoparasitic bees in the Afrotropical region. Nonetheless, the discovery of a new and distinctly different species allows us to refine the diagnosis of the genus and re-evaluate characters that were previously thought to be diagnostic. First, the pre-apical tooth described as diagnostic for the genus (Eardley 2009) is lacking in *S. elizabethae*. The mandible is unidentate in both sexes; there may only be a very slight elevation on the inner margin of the mandible. The structure is different from the truly bidentate mandibles of presumably closely related species of Biastini, such as *B. brevicornis* (Panzer, 1798) or *B. emarginatus* (Schenck, 1853). Eardley (2009) further noted that the first recurrent vein meets the first submarginal crossvein at the posterior margin of the submarginal cells in the forewing (e.g., Fig. 6C). While this character holds up for *S. emmae*, it is more variable in *S. elizabethae*, with some individuals having this character, while in others the first recurrent vein merges distal to the submarginal crossvein. However, examination of both species of *Schwarzia* revealed two additional diagnostic features. First, all individuals have conspicuously broadened tibial spurs which possess two ventral rows of minute teeth. This character is most obvious for the large inner metatibial spur and is somewhat similar to the modified tibial spur of *Austrosystropha* Patiny & Michez, 2006, a subgenus of *Systropha* Illiger, 1806 (Patiny et al. 2013, Patiny and Michez 2006), and certain species of *Neopasites* (e.g., *N. cressoni* Crawford, 1916; *N. fulviventrtris* (Cresson, 1878)). Second, males of *Schwarzia* only have 10 flagellomeres. As described in the etymology section, males of most known bee species have 11 flagellomeres (= 13 antennal segments, including scape and pedicel) and females have 10 (= 12 antennal segments).

The reduced number of antennal segments in *Schwarzia* males is indicative of a close relationship to other Biastini. Reduced flagellomeres of males are generally rare in bees but occur more frequently in certain tribes of cleptoparasitic Apidae. In Ammobatini, males of *Pasites* Jurine, 1807, *Melanempis* Saussure, 1890, *Parammobatodes* Popov, 1932 and *Chiasmognathus* Engel, 2006 have reduced numbers

of flagellomeres (Eardley and Brothers 1996, Engel and Packer 2013, Michener 2007, Pauly et al. 2001), and so do *Neopasites* (e.g., *N. cressoni*, *N. fulviventris*), and certain *Biastes* (e.g., *B. brevicornis*, *B. emarginatus*) in Biastini. Some species of *Holcopasites* Ashmead, 1899 (Ammobatoidini), such as *H. heliopsis* (Robertson, 1897) or *H. haematurus* Cockerell & Hicks, 1926, have reduced male antennae as well. Further, all these bees have usually just two submarginal cells, both characteristics that could indicate a closer relationship to *Schwarzia*. However, the labrum of *Schwarzia* is clearly broader than long, a decisive characteristic which delineates the Biastini from all the aforementioned bees. I therefore follow Eardley's (2009) understanding that *Schwarzia* is most likely a lineage of Biastini. Furthermore, I argue that even though the morphology of the females' fifth tergum is clearly derived, the large projections could actually be homologous to the much smaller posterolateral projections on the fifth tergum of certain species *Biastes* or *Neopasites*, such as a *B. brevicornis*, or *N. fulviventris* (Fig. 7).

An interesting and prominent morphological difference between *S. emmae* and *S. elizabethae* are the finely punctate supraclypeal protrusions of *S. emmae*, which are entirely absent in *S. elizabethae* (Figs 2C-D, 4C-D). Very similar morphological structures occur in several not closely related bees, such as diverse species of *Epeolus* Latreille, 1802 (e.g., *E. bifasciatus* Cresson, 1864, *E. boliviensis* Friese, 1908; Onuferko 2017, Onuferko 2018), *Holcopasites* (*H. bigibbosus* Hurd & Linsley, 1972) or *Chilicola* Spinola, 1851 (e.g., *Chilicola obesifrons* Packer, 2007; Packer and Genaro 2007). Certain species of the *Coelioxys* Latreille, 1809 subgenera *Synocoelioxys* Mitchell, 1973 (e.g., *Coelioxys apacheorum* Cockerell, 1900, *Coelioxys texana* Cresson, 1872) and *Glyptocoelioxys* Mitchell, 1973 bear granulose swellings around the median ocellus, which are similar in surface structure to protrusions of aforementioned taxa. As all these taxa are quite distantly related, it can be assumed that these features evolved independently and that they are not necessarily similar in function. However, while the exact function of any of these protrusions is unknown, it seems plausible that they may be involved in sensory perception or processing. Interestingly, all bees but *Chilicola* are cleptoparasites, which indicates that the evolution of such protrusions may at least be favored in bees that do not collect pollen, but search and parasitize nests of host bees.

Potential hosts of *Schwarzia*

Due to the lack of field observational data for *Schwarzia*, the biology of both species is essentially unknown. All presently available material was collected with traps and therefore no information on flower visitation or potential host(s) is available. Nonetheless, the morphology and presumably close phylogenetic relationship to *Biastes* leaves no doubt that *Schwarzia* has a cleptoparasitic lifestyle. All Biastini are cleptoparasites of species of Rophitinae (Michener 2007), and Eardley (2009) singles out *Systrophia* as the only rophitine genus in Eastern Africa. *Systrophia* is common in Eastern Africa (Eardley 2009) and at least five species are known from Kenya or directly adjacent

countries (Ascher and Pickering 2019, Bossert and Patiny 2017, Patiny et al. 2013, Patiny and Michez 2006), with likely more species to be documented.

Schwarzia and the potential host *Systropha* even share certain morphological features: both sexes have an unusually long glossa, which is rather uncommon for cleptoparasitic bees. The long mouthparts suggest that *Schwarzia* bees collect nectar at flowers with a deep corolla, and therefore may even visit the same flowers as their potential host *Systropha*, which are specialists on flowers of the morning glory family (Convolvulaceae; Michener 2007, Patiny et al. 2008). Nonetheless, no specimen of *Systropha* was collected during the same trap collecting events coincident with the specimens of *Schwarzia* examined in this study. Bees of the following genera were collected with *Schwarzia*:

Collecting event 1 (near the Sarara Camp, 10.-13.VI.1998; collection site of *S. emmae*): *Afranthidium* Michener, 1949, *Amegilla* Friese, 1897, *Braunsapis* Michener, 1969, *Ceratina* Latreille, 1802, *Macrogalea* Cockerell, 1930, *Macronomia* Cockerell, 1917, *Maynenomia* Pauly, 1984, *Nubenomia* Pauly, 1980, *Seladonia* Robertson, 1918, *Thrinchostoma* de Saussure, 1890.

Collecting event 2 (in Tsavo East National Park, 10.VI.1998; collection site of *S. emmae*): *Acunomia* Cockerell, 1930, *Afromelecta* Liefstinck, 1972, *Amegilla*, *Anthidium* Fabricius, 1804, *Ceratina*, *Coelioxys*, *Lasioglossum* s.l. Curtis, 1833, *Lipotriches* Gerstaecker, 1858 subgenus *Patellotriches* Pauly, 2014, *Lipotriches* subgenus *Stellotriches* Pauly, 2014, *Macronomia*, *Megachile* Latreille, 1802, *Meganomia* Cockerell, 1909, *Mermiglossa* Friese, 1912, *Nubenomia*, *Pseudapis* (s. str.) Kirby, 1900, *Seladonia*, *Sphecodes* Latreille, 1804, *Thyreus* Panzer, 1806.

Collecting event 3 (in Tsavo East National Park, 22.-29.XI.1999; collection site of *S. elizabethae*): *Amegilla*, *Braunsapis*, *Coelioxys*, *Lipotriches* subgenus *Stellotriches*, *Macrogalea*, *Maynenomia*, *Megachile*, *Pasites* Jurine, 1807, *Pseudapis* (s. str.).

Collecting event 4 (in Tsavo East National Park, 29.III-1.IV.1999; collection site of *S. elizabethae*): *Pasites*.

Non-parasitic bees were only collected in collecting events 1, 2, and 3. The only bee genus that was collected during all these three events is *Amegilla*, an apid bee genus in the subfamily Anthophorinae (Bossert et al. 2019). However, since *Amegilla* is diverse, common, and widespread throughout Africa (Eardley et al. 2010), it is quite likely that these findings are simply a representation of the abundance of *Amegilla* at those sites, and do not necessarily reflect a host-parasite relationship. Most bees of the genus *Amegilla* are also much larger than the species of *Schwarzia*, and all collected specimens of *Amegilla* significantly exceeded the size of *Schwarzia*. In the future, field observational efforts in Eastern Africa are required to shed light on the potential host of *Schwarzia*, in order to better understand the biology of these intriguing bees.

Acknowledgments

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