RESEARCH ARTICLE



New genera of meliturguline bees from Saudi Arabia and Persia, with notes on related genera and a key to the Arabian fauna (Hymenoptera: Andrenidae)

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Abstract

A new genus of melitturgine bees (Panurginae: Melitturgini) is described and figured from central Saudi Arabia. *Belliturgula najdica* Engel, **gen. et sp. n.**, is similar in several respects to the genus *Flavomeliturgula* Patiny in that both have a greatly elongate glossa that is longer than the face and is truncate apically. The former differs in the greatly elongate and flattened first labial palpomere, the remaining palpomeres unmodified, the greatly protuberant clypeus, and long labrum lacking dense setal patches, among other traits. In addition, remarks are made on the composition of *Flavomeliturgula*, with *Meliturgula deserta* Warncke (Iran, Pakistan), removed to *Khuzimelissa* Engel, **gen. n.**, resulting in the new combination *Khuzimelissa deserta* (Warncke), **comb. n.** *Khuzimelissa* differs from *Flavomeliturgula* by the unmodified labial palpomeres (lacking the elongate first three labial palpomeres of the latter genus), the acute glossa (broadly truncate in the latter), glossa shorter than head length (greater than head length in the latter), the abundant, white, squamiform setae of the mesoscutum (sparse, erect setae in the latter), cleft pretarsal claws (simple in the latter), presence of metasomal setal bands (lacking in the latter), and apically emarginate pygidial plate (acutely rounded in the latter). The species of *Flavomeliturgula* are organized into three subgenera, including *Koreshomelissa* Engel, **subgen. n.**, and *Freyamelissa* Engel, **subgen. n.**, and these may eventually warrant generic status once phylogenetic work on the tribe has been completed. A key to the Arabian genera of Panurginae is provided, along with an augmented key to the genera of subtribe Meliturgulina.

Keywords

Anthophila, Apoidea, Arabia, Melitturgini, Meliturgulina, Panurginae, taxonomy

Introduction

Bees of the panurgine tribe Melitturgini are uncommonly encountered in the Arabian fauna. Hitherto, the tribe has been represented in Arabia by only four species in two genera: *Meliturgula scriptifrons* (Walker) (=*Poecilomelitta dzheddaensis* Popov), *M. ornata* (Popov), *Borgatomelissa brevipennis* (Walker) (= *Nomia eburneifrons* Walker, *M. arabica* Popov), and *B. niveopilosa* Patiny (Walker 1871; Popov 1951; Patiny 2002). The biology of these bees in Arabia remains unstudied, and even basic records of floral associations are lacking. The latter two species have been considered related to *Melitturga* Latreille and segregated into a nominate subtribe, while the species of *Meliturgula* Friese are classified in the subtribe Meliturgulina. Three genera have been recognized in Meliturgulina: *Gasparinahla* Patiny, known only from a single, poorly preserved male from southwestern Iran; *Flavomeliturgula* Patiny, encompassing several species occurring across southern Iran and Pakistan; and *Meliturgula*, the largest genus of the group, with species distributed throughout Arabia and Africa but concentrated in southern Africa (Michener 2007).

Here we report a new species of meliturguline for the Arabian fauna, representing a new genus. Individuals of the species were found collecting pollen from *Carthamus* L. (Asteraceae: Carduoideae: Cynareae) in central Saudi Arabia (Figs 1, 2). The new species is somewhat similar to some species hitherto classified in *Flavomeliturgula*. We provide the description of the new taxon, along with notes on the systematics of *Flavomeliturgula* (e.g., Table 1). The new species as well as several of those hitherto classi-

Genus Khuzimelissa Engel, gen. n.		
K. deserta (Warncke, 1983 [1985])	Iran (Khuzestan), Pakistan (Balochistan)	
Genus Belliturgula Engel, gen. n.		
B. najdica Engel, sp. n.	Saudi Arabia (Riyadh)	
Genus Flavomeliturgula Patiny, 1999		
Subgenus <i>Flavomeliturgula</i> s.str.		
F. lacrymosa (Popov, 1967)	Iran (Khuzestan, Hormozgān, Fars, Tehran)	
Subgenus Freyamelissa Engel, subgen. n.		
F. schwarziana Patiny, 2004	Pakistan (Balochistan)	
F. berangeriae Patiny, 2002	Iran (Bushehr)	
Subgenus Koreshomelissa Engel, subgen. n.		
F. tapana (Warncke, 1983 [1985])	Iran (Māzandarān)	
F. centaurea (Warncke, 1983 [1985])	Iran (Hormozgān), Pakistan (Balochistan)	

 Table 1. Current classification of species discussed herein.



Figures 1, 2. Female of *Belliturgula najdica* Engel, gen. et sp. n., at flowers of *Carthamus* L. (Asteraceae) in central Saudi Arabia.

fied in *Flavomeliturgula* are as different from one another as are traditionally differentiated as distinct genera among bees, particularly among different lineages of Panurginae (e.g., Ruz 1986, 1991; Patiny 2001; Roig-Alsina and Compagnucci 2003; Gonzalez and Engel 2011; Gonzalez et al. 2013, 2017; Ramos and Rozen 2014). Aside from differences in setation, coloration, and the shape of labra, sulci, pygidial plates, and other structural distinctions, the development of the mouthparts are strikingly different among these groups, and this may reflect some degree of difference in host plant visitation or specialization, much as is observed among other panurgine genera (e.g., Rozen and Ruz 1995; Rozen 2003). Accordingly, the classification is augmented in order to reflect and highlight these differences, and encourage melittologists to see out the biology of these rather different groups. In addition, we provide keys to the genera of Arabian Panurginae and to the genera of subtribe Meliturgulina.

Material and methods

The morphological terminology for the systematic work is largely taken from Engel (2001) and Michener (2007). Photographs were taken with a Canon 7D digital camera attached to an Infinity K-2 long-distance microscope lens, illuminated with a Xenon flash, while measurements were taken with an ocular micrometer on an Olympus SZX12 stereomicroscope. Specimens were examined from the collections of the Division of Entomology (Snow Entomological Collections), University of Kansas Natural

History Museum, Lawrence, Kansas, USA (**SEMC**); the King Saud University Museum of Arthropods, Plant Protection Department, College of Food and Agriculture Sciences, King Saud University, Riyadh, Kingdom of Saudi Arabia (**KSMA**); and the Division of Invertebrate Zoology, American Museum of Natural History, New York, New York, USA; while types for the new species described herein are deposited in the former two institutions.

Systematics

Tribe Melitturgini Newman, 1834 Subtribe Meliturgulina Engel, 2001

Belliturgula Engel, gen. n.

http://zoobank.org/896747C8-0BD5-4B8B-8DBA-3C33E1CC588A

Type species. Belliturgula najdica Engel, sp. n.

Diagnosis. The genus resembles *Flavomeliturgula* in the elongate and apically truncate glossa but differs in the following attributes: body almost entirely pale yellow, with scattered dark brown to black markings; outer subantennal sulcus arched; clypeus greatly protuberant and extending well in front of compound eyes; labrum as long as wide, with distinct basilateral ovoid windows of translucent integument; proximal labial palpomere greatly elongate and flattened, twice as long as combined length of remaining palpomeres, extending well past apex of paraglossa; second through fourth labial palpomeres cylindrical, not flattened; apex of glossa not broadened; galea longer than stipes; mesoscutum covered with abundant, erect, minutely spicate, white setae; forewing 1rs-m confluent with (rather than distad) 1m-cu; basal area of propodeum setose; probasitarsus short and broad, about twice as long as wide; mesotibial spur short, only about 0.5× length of mesobasitarsus; pygidial plate with margins concave apically and therefore more abruptly tapering to acutely rounded apex.

Description. Small species (less than 8 mm in total length); integument largely yellow, with some dark brown to black markings (Figs 1–5); head broader than long; compound eyes with inner margins parallel (Fig. 5); outer subantennal sulcus greatly arched outward (Fig. 5) (not straight); facial fovea shallow, narrower than median ocellar diameter, elongate, length approximately $5.5 \times$ width (Fig. 5); clypeus greatly protuberant, extending in front of compound eye by almost as much as compound eye width (Fig. 8) (protuberance extending in front of compound eye by distance approximately $0.85-0.95 \times$ compound eye width); labrum as long as wide, with basilateral ovoid areas ('windows') of translucent integument, without basilateral patches of dense, elongate, branched setae, with shallow, mediolongitudinal depression; ventral surface of prementum without abundant, long, posteriorly directed, simple setae (such setae present in *Khuzimelissa*); first labial palpomere greatly elongate and flattened, much longer than remainder of palpus (Fig. 12) (2× as long as combined lengths of remaining palpomere



Figures 3, 4. Female of *Belliturgula najdica* Engel, gen. et sp. n., from central Saudi Arabia. 3 Lateral habitus 4 dorsal habitus.

es), extending greatly beyond apex of paraglossa, second palpomere not flattened, third through fourth palpomeres short, subequal in length, cylindrical (Fig. 12); glossa greatly elongate, distinctly longer than face (Fig. 8); apex truncate but not broadened (Fig. 9); galea longer than stipes (galea slightly longer than stipes in *Flavomeliturgula*; galea shorter than stipes in *Khuzimelissa*); mesoscutum with numerous scattered, erect, minutely spicate (pipecleaner-like in appearance), white setae, not obscuring integument (0.8–1.3×



Figures 5-7. Female faces of representative Meliturgulina. 5 *Belliturgula najdica* Engel, gen. et sp. n., from Saudi Arabia (note arched outer subantennal sulci) 6 *Khuzimelissa deserta* (Warncke), comb. n., from Pakistan 7 *Flavomeliturgula (Flavomeliturgula) lacrymosa* (Popov) from Iran (note straight outer subantennal sulci).

median ocellar diameter) (Fig. 4); basal area of propodeum setose, setae not obscuring integument; forewing with pterostigma longer than wide, approximately 3.5× as long as wide, width subequal to length of prestigma, about 3.5× as long as prestigma, margin bordering first submarginal cell slightly diverging from anterior wing margin, border inside marginal cell converging toward anterior wing margin and with convex arch; marginal cell widely and slightly obliquely truncate at apex, longer than distance from its apex to wing tip; three submarginal cells present (i.e., 1rs-m present); length of first submarginal cells; r-rs

and 3Rs (anterior border of second submarginal cell) subequal; 2Rs and 1rs-m slightly converging anteriorly, thus second submarginal cell trapezoidal; 3Rs slightly longer than 0.5× 4Rs (anterior border of third submarginal cell); 1rs-m confluent with 1m-cu (as in Gasparinhala); 1cu-a at least 2× as long as 2M+Cu (usually 2M+Cu even shorter in other genera); hind wing with six distal hamuli; probasitarsus broad, about twice as long as wide (probasitarsus more elongate slender in *Flavomeliturgula*, nearly four times as long as wide); protibial calcar with velum rectangular, velum with outer and apical borders comparatively straight, malus (apical portion of rachis: sensu Engel et al., 2017) ciliate and slightly shorter than velum; mesofemur ventro-proximally forming nearly orthogonal angle (as in *Flavomeliturgula*, *Meliturgula*, *Khuzimelissa*, and related genera); mesotibial spur serrate, about 0.5× length of mesobasitarsus; metabasitibial plate broadly rounded, with carinate margins and surface covered in appressed, minute, plumose setae; metatibial and metabasitarsal scopa composed of abundant, elongate (1.8-3.2× median ocellar diameter), simple setae; pretarsal claws simple; metasomal terga without well-developed setal bands (Fig. 4) (present in Khuzimelissa); pygidial plate with apex narrowly rounded, margins tapering more prominently in apical half (Fig. 24).

Etymology. The generic name is an artificial combination of Bell, honoring explorer, archeologist, and nation-builder Gertrude Margaret Lowthian Bell (1868–1926), and a subset of *Meliturgula* Friese, type genus of the subtribe Meliturgulina. The name is therefore treated as a euphonious combination of letters and the gender of the name is considered to be feminine.

Included species. The genus includes at present only the type species, found in central Saudi Arabia.

Belliturgula najdica Engel, sp. n.

http://zoobank.org/145B107D-91C2-424D-A736-5521CD3FF7DD Figs 1–5, 8, 9, 12, 24

Diagnosis. As for the genus (*vide supra*).

Description. \bigcirc : Total body length 7.08–7.33 mm; forewing length 4.13–4.27 mm. Head broader than long, width 2.08–2.13 mm, length 1.67–1.71 mm; compound eyes with inner orbits margins roughly parallel, upper interorbital distance 1.33–1.38 mm, lower interorbital distance 1.33–1.36 mm; distance between compound eyes slightly greater than compound eye length; compound eye length 1.25 mm, width 0.58–0.63 mm; clypeus greatly protuberant, extending in front of compound eye by nearly compound eye width; intertegular distance 1.42–1.46 mm.

Clypeus and supraclypeal area largely smooth with coarse, shallow (almost faint in most areas) punctures, such punctures separated by a puncture width or more, slightly denser along borders; labrum similar to clypeus except impunctate on transparent ovals; remainder of face similar except punctures smaller, more defined (albeit still shallow), and separated by a puncture width or frequently less; dark area between ocelli minutely and faintly imbricate and impunctate; facial fovea imbricate and impunctate; gena as on



Figures 8–11. Female heads and mouthparts in profile and details of glossal apexes. **8** Head profile of *Belliturgula najdica* Engel, gen. et sp. n., from Saudi Arabia **9** glossal apex of *B. najdica* **10** head profile of *Flavomeliturgula (Flavomeliturgula) lacrymosa* (Popov) from Iran **11** glossal apex of *F. (F.) lacrymosa*.

upper face except punctures becoming more sparsely separated ventrally; mesoscutum smooth to faintly and minutely imbricate with shallow punctures separated by a puncture width or less; mesoscutellum as on mesoscutum except punctures slightly denser and integument slightly more noticeably imbricate; metanotum as on mesoscutellum except shallow punctures nearly contiguous; pleura as on mesoscutum except punctures shallower and becoming sparse ventrally; basal area of propodeum as on metanotum; lateral and posterior surfaces of propodeum with small punctures separated by a puncture width or frequently less, integument between punctures smooth to faintly imbricate; metasomal terga minutely and finely imbricate with scattered shallow, faint, small punctures separated by a puncture width or less, such punctures most easily discernible on first tergum and becoming fainter on succeeding terga; pygidial plate minutely and finely imbricate; sterna as on terga except shallow, coarse punctures more prominent.

Integument generally pale yellow except marked with dark brown to black on mandibular apex, on facial fovea, around ocelli (Figs 4, 5); mesoscutum with three longitudinal dark stripes, medial stripe thin, terminating before posterior of mesoscutum, lateral stripes thicker, situated between lateral yellow borders and medial stripe, extending to axilla (Fig. 4); dark brown on lateral depression of axilla and along anterior border of mesoscutellum (slightly extended mediolongitudinally) (Fig. 4), and light brown anteriorly on basal area of propodeum (Fig. 4). Wing membranes clear, hyaline; veins pale yellow to off white (Fig. 3). Metasoma with light to dark brown marks as follows: paramedian spots on anterior-facing surface of first metasomal tergum (Fig. 4), elongate oval spots at lateral extremities of second tergum (Fig. 3), small spots on lateral extremities of third tergum (absent in some individuals); terga I–V with irregular brownish-purplish coloration (reflective of inner organs through pale integument) to varying degrees (in some individuals inner gut prominent through integument, others less so); pygidial plate brown, becoming reddish apically (Fig. 24); sterna pale brown, becoming darker on two apical sterna.

Pubescence generally white and largely sparse (Figs 3-5); facial setae generally short to moderate (0.2-1.0× median ocellar diameter) in length and minutely spicate (i.e., minutely branched on all sides along entire length of rachis, with a pipecleaner-like appearance), such setae scattered on face and generally suberect; scape with similar moderate-length, erect, minutely spicate setae; minutely spicate setae longer (0.9–1.5× median ocellar diameter) and erect around ocelli, vertex, posterior of gena, and postgena; mandible with more sparse, elongate (1.8-3.0× median ocellar diameter), simple setae along lower margin; mesoscutum with numerous erect short to moderate-length (0.4-1.2× median ocellar diameter) minutely spicate setae, such setae not obscuring integument; mesoscutellum as on mesoscutum although setae slightly sparser; metanotum with minutely spicate setae sparse on disc, with various greatly elongate (up to 2.0× median ocellar diameter) minutely spicate setae at lateral extremities; pleura with numerous moderate-length to elongate (1.0-2.2× median ocellar diameter) minutely spicate setae, such setae not obscuring integument; basal area of propodeum with numerous fine minutely spicate setae, not obscuring integument; propodeum with lateral and posterior surfaces with pubescence similar to that of pleura; legs with minutely spicate setae except simple on tarsi and scopal setae of metatibia and metabasitarsus elongate (1.8-3.2× median ocellar diameter) and simple; metasoma with generally sparse pubescence, setae more numerous on apical terga where such setae minutely spicate and suberect to erect; setae particularly dense around pygidial plate and obscuring integument.

 \mathcal{O} : Latet.



Figures 12–15. Labial palpi of representative species (to same scale) and labiomaxillary complex of *Khuzimelissa deserta* (Warncke), comb. n. (not to same scale), all in ventral view. 12 Labial palpus of *Belliturgula najdica* Engel, gen. et sp. n. 13 labial palpus of *K. deserta* 14 labial palpus of *Flavomeliturgula* (*Flavomeliturgula*) lacrymosa (Popov) 15 photograph of labiomaxillary complex of *K. deserta*.

Holotype. \mathcal{Q} , KSA [Kingdom of Saudi Arabia], Riyadh [Region], Derab Agricultural Research Station [24°25'23"N, 46°39'01"E, 580 m elevation], 29.4.2015 [29 April 2015], M. Shebl, *Carthamus* [Asteraceae: *Carthamus* L.] (SEMC).

Paratypes. $2 \stackrel{\bigcirc}{\downarrow} \stackrel{\bigcirc}{\downarrow}$, same data as holotype (SEMC, KSMA).

Etymology. The specific epithet is taken from the Najd, the vast geographic central plateau portion of Saudi Arabia which encompasses the type locality which is slightly south of the city of Riyadh.

Comments. The type series was collected from an unidentified species of distaff thistle (Asteraceae: Carduoideae: *Carthamus* L.) growing around the Dirab Agricultural Research Station in central Saudi Arabia (just south from Riyadh). The most common species of *Carthamus* in Saudi Arabia are *Carthamus oxyacantha* M.Bieb., which grows wild in many disturbed areas, and *C. tinctorius* Linnaeus (safflower), the latter widely cultivated, particularly so in southern Arabia (Mandaville, 1990). It is likely that the type series of *B. najdica* was captured at *C. oxyacantha*. Species of *Carthamus* are spiny, dentate herbs that can be largely self-pollinated, although among insects bees are the dominant pollinators (e.g., Butler et al., 1966).

Khuzimelissa Engel, gen. n.

http://zoobank.org/FF287D5A-51DA-4BE4-A353-B1B896BB858D

Type species. Meliturgula deserta Warncke, 1983 [1985].

Diagnosis. The genus superficially resembles *Flavomeliturgula* and *Belliturgula*, particularly the latter in the extensive yellow coloration. However, the genus differs from both in the short, more typical labial palpomeres in which the proximal labial palpomere is elongate, flattened, longer than the combined lengths of the remaining palpomeres (approximately 1.25× length of remaining palpomeres combined), with the second palpomere flattened and slightly shorter than the length of the third and fourth palpomeres combined; and the third and fourth palpomeres subequal in length and cylindrical (Fig. 13). In addition, the glossa is acute (Figs 6, 15) (rather than broadly truncate apically), the glossa is shorter than the head length (Figs 6, 19–21) (rather than greater than the head length in the former two genera), the pretarsal claws are cleft (simple in the former two genera), the metasomal terga have distinctive broad setal bands (Figs 16–18) (lacking in the former two genera), and the pygidial



Figures 16–18. Female of *Khuzimelissa deserta* (Warncke), comb. n., from Pakistan. 16 Dorsal habitus 17 lateral habitus 18 detail of mesosoma and anterior metasomal dorsum.



Figures 19–21. Female of *Khuzimelissa deserta* (Warncke), comb. n., from Pakistan. 19 Head and mouthparts in profile 20 dorsal-frontal view of mouthparts 21 extended labiomaxillary complex in profile.

plate is apically emarginate (Fig. 25) (acutely rounded in the former two genera). Other diagnostic traits include: small species, slightly more than 8 mm in length; integument largely pale yellow with few dark brown to black markings (Figs 6, 16–18); outer subantennal sulcus arched (Fig. 6); clypeus gently and weakly convex, scarcely protuberant (Figs 6, 17, 19), extending in front of compound eye by about 0.5× com-



Figures 22, 23. Female of *Flavomeliturgula* (*Flavomeliturgula*) *lacrymosa* (Popov) from Iran. 22 Dorsal habitus 23 lateral habitus.

pound eye width; labrum wider than long, width $1.7 \times$ length, without lateral oval windows of transparent integument (Fig. 20), surface gently and weakly convex with weak subtriangular proximal medial depression; prementum ventrally with abundant, elongate $(1.0-1.9 \times$ median ocellar diameter), erect to suberect, simple setae (Figs 15, 19, 21); galea shorter than stipes; mesoscutum with abundant, appressed, squamose setae (Fig. 18), intermixed with sparse, erect, minutely spicate setae $(0.8-1.0 \times$ median ocellar diameter); probasitarsus elongate, slender, length approximately $3 \times$ width; mesotibial spur about as long as mesobasitarsus; forewing with r-rs distinctly shorter



Figures 24–26. Female pygidial plates. 24 Belliturgula najdica Engel, gen. et sp. n. 25 Khuzimelissa deserta (Warncke), comb. n. 26 Flavomeliturgula (Flavomeliturgula) lacrymosa (Popov).

than 3Rs, 1rs-m distad 1m-cu, and 1cu-a about 4× as long as 2M+Cu; hind wing with 10 or more distal hamuli arranged in a dense series.

Etymology. The new genus-group name is a combination of Khuzi, the Middle Persian name for the ancient Susian people, and from which the regional name Khuzestan derives (and encompasses the type locality of the type species), and the Greek, *mélissa* ($\mu \epsilon \lambda \iota \sigma \sigma \alpha$), meaning, "bee". The gender of the name is feminine.

Included species. The genus presently includes only the type species, *Khuzimelissa deserta* (Warncke), comb. n., which has been recorded from Iran (Khuzestan) and Pakistan (Balochistan).

Genus Flavomeliturgula Patiny

Diagnosis. The genus can be generally differentiated from other members of the subtribe by the following combination of features: small to medium-sized bees, 5.0–10.0 mm in length; integument dark brown to brown with extensive yellow mark-

15

ings (Figs 22, 23); outer subantennal sulcus straight (Fig. 7); clypeus weakly protuberant, extending in front of compound eye by about 0.35-0.5× compound eye width (Fig. 10); labrum wider than long, width 1.5× length, without lateral oval windows of transparent integument, surface with weakly raised, medial plateau, basilaterally with prominent setose patches composed of long (1.8-2.4× median ocellar diameter), subdecumbent setae; prementum ventrally without elongate setae; proximal labial palpomere elongate (but not extending past apex of paraglossa: in Belliturgula palpomere extends well past apex of paraglossa), flattened, about as long as to slightly longer than combined lengths of remaining palpomeres; second and third palpomeres flattened and elongate, together slightly shorter than to about as long as first palpomere, fourth palpomere short, shorter than preceding palpomere, cylindrical combined (Fig. 14); glossa greatly elongate, longer than head length, apex broadly truncate and broadened (Figs 7, 10, 11); mesoscutum without appressed, squamose setae or abundant spicate setae (Fig. 22); forewing with 1rs-m distad 1m -cu (confluent in Belliturgula); probasitarsus elongate, slender, length approximately 4× width; mesotibial spur elongate, nearly 0.75× as long as mesobasitarsus; pretarsal claws simple; metasomal terga without distinctive broad setal bands; pygidial plate apically acutely rounded, with lateral margins tapering evenly toward apex, surface with mediolongitudinal ridge (Fig. 26).

Key to Subgenera of Flavomeliturgula

1	Propodeum basal area without setae; hind wing with 10 or more distal ha-
	muli arranged in a dense series Flavomeliturgula Patiny, s.str.
_	Propodeum basal area with distinct setae; hind wing with 6–7 distal hamuli.
2(1)	Mesoscutum brown to black with yellow markings; mesoscutum with min-
	ute, scattered setae, length of setae distinctly less than 0.5× median ocellar
	diameter Koreshomelissa Engel, subgen. n.
_	Mesoscutum entirely black, without yellow markings; mesoscutum with scat-
	tered, white setae, particularly anteriorly, length of setae 1–1.5× median ocel-
	lar diameter Freyamelissa Engel, subgen. n.

Subgenus Flavomeliturgula Patiny

Meliturgula (*Flavomeliturgula*) Warncke, 1983 [1985]: 229, *nomen invalidum* (no type species designated: ICZN 1999: Art. 13.3). *Nota bene*: Michener (2007) erroneously indicated the name as used by Warncke was a *nomen nudum* and included no species. In fact, Warncke did include four species and even provided scant diagnostic traits for the group (meaning it was not a *nomen nudum*), but only failed to explicitly designate a type species. *Flavomeliturgula* Patiny, 1999: 251. Type species: *Poecilomelitta lacrymosa* Popov, 1967, by original designation.

Diagnosis. The subgenus can be distinguished by the combination of: mesoscutum dark brown to black with yellow markings, surface with scattered, appressed, fine setae, such setae mostly anteriorly and laterally, and $0.5-0.75 \times$ median ocellar diameter; basal area of propodeum without setae; and hind wing with 10 or more distal hamuli arranged in a dense series along anterior wing margin.

Included species. The subgenus as here circumscribed is restricted to the type species, *Flavomeliturgula lacrymosa* (Popov), from Iran (Fars, Hormozgān, Khuzestan, Tehran).

Koreshomelissa Engel, subgen. n.

http://zoobank.org/9A888F48-0556-4243-A804-07000235BB63

Type species. Meliturgula tapana Warncke, 1983 [1985].

Diagnosis. The subgenus can be distinguished by the combination of: mesoscutum dark brown to black with yellow markings, surface with scattered, minute, fine setae, and less than 0.5× median ocellar diameter; basal area of propodeum with setae; and hind wing with 6–7 distal hamuli along anterior wing margin.

Etymology. The new subgeneric name is a combination of Kóréš or Kūruš, the Hebrew and Persian names for Cyrus the Great (Cyrus II, ca. 600–530 B.C.), who first unified the ancient kingdoms of the Near East and founded the Achaemenid Empire of Persia, combined with the Greek, *mélissa* (μ έλισσα), meaning, "bee". The gender of the name is feminine.

Included species. The subgenus includes two species: *F. (Koreshomelissa) tapana* and *F. (K.) centaurea* (Warncke), both from northern (along the Caspian Sea) and southern costal Iran (Māzandarān and Hormozgān) and southern Pakistan (Balochistan).

Freyamelissa Engel, subgen. n.

http://zoobank.org/6F683DEC-CFBB-4FFA-B998-9D4333967A4B

Type species. Flavomeliturgula berangeriae Patiny, 2002.

Diagnosis. The subgenus can be distinguished by the combination of: mesoscutum entirely black without yellow maculation, surface with scattered setae of $1-1.5 \times$ median ocellar diameter; basal area of propodeum with setae; and hind wing with 6-7 distal hamuli along anterior wing margin.

Etymology. The new subgeneric name is a combination of Freya, for the famed explorer of Arabia, Persia, and Afghanistan, Freya Madeline Stark (1893–1993), and the Greek, *mélissa* (μέλισσα), meaning, "bee". The gender of the name is feminine.

Included species. The subgenus includes two species: F. (*Freyamelissa*) berangeriae and F. (F) schwarziana Patiny, from southwestern Iran (Bushehr) and southern Pakistan (Balochistan).

Key to Genera of Saudi Arabian Panurginae

1	Forewing with two submarginal cells2
_	Forewing with three submarginal cells
2(1)	S6 of male with posterior margin thin and more or less straight or usually
	broadly bilobed but usually without an apical zone of very short setae; epis-
	ternal groove present but usually short, not reaching level of scrobe, or rarely
	absent: 1m-cu distal to 1rs-m, joining second submarginal cell
	Panurous Panzer
_	S6 of male with posterior margin slightly to strongly produced medially, this
	projection with truncate to broadly concave apex margined by zone of short
	setae: episternal groove entirely absent (body entirely black except for yellow
	clypeus of some males; 1m-cu meeting or basal to 1rs-m or nearly so
	Panurginus Nylander
3(1)	First labial palpomere greatly elongate and flattened, much longer than re-
- ()	mainder of palpus, third through fourth palpomeres short, subequal in
	length, cylindrical: glossa longer than face, with apex truncate: body wholly
	vellow with few black markings on head and mesosomal dorsum
	Relliturgula Engel gen n
_	First labial palpomere elongate as long as or longer than second to fourth
	palpometer together: glossa pointed: body variable mostly dark never wholly
	vallow
(3)	Mesoscutum of famile densely covered with short thickened appressed setae
4(J)	among which are scattered erect solar male genestylus yery slander as long as
	among which are scattered erect setae; male gonostylus very siender, as long as
	gonocoxite; voisella spiculate, extending beyond gonocoxites; seventh meta-
	somal tergum of male with bind apex; sixth and seventh metasomal sterna of
	male with deep medioapical emarginationsBorgatomeiissa Patiny
-	Mesoscutum of female with scattered suberect setae or in some species with
	appressed setae, less dense than as above; male gonostylus robust, half as long
	as gonocoxite or less; volsella not spiculate, extending little if at all beyond
	gonocoxites; seventh metasomal tergum of male with apex simple; sixth and
	seventh metasomal sterna of male with apical margins transverse or convex

Key to Genera of Meliturgulina

1	Glossa shorter than face
_	Glossa longer than face
2(1)	Body largely yellow; pygidial plate of female emarginate apically, surface with
	weak mediolongitudinal ridge, faintly imbricate
_	Body largely black with areas of yellow maculation; pygidial plate of female
	rounded apically, surface flat, imbricate Meliturgula Friese

3(1)Glossal apex broadly truncate; maxillary palpus with six palpomeres.......4 Glossal apex acute; maxillary palpus apparently vestigial ("nearly absent" ac-Proximal labial palpomere greatly elongate, more than 2× as long as com-4(3)bined lengths of remaining palpomeres, extending greatly beyond apex of paraglossa; remaining palpomeres not flattened; outer subantennal sulcus of female greatly arched; female clypeus greatly protuberant, in profile extending in front of compound eye by about compound eye width; female labrum as long as wide, without medioapical elevated plateau and without basilateral patches of dense, long, branched setae Belliturgula Engel, gen. n. Proximal three labial palpomeres long, flattened; first labial palpomere not extending past apex of paraglossa, shorter than combined lengths of remaining palpomeres; outer subantennal sulcus straight; clypeus weakly protuberant, in profile extending in front of compound eye by much less than compound eye width; female labrum wider than long, with medioapical elevated circular or ovoid plateau, with basilateral patches of dense, long, branched setae

Discussion

The diversity of bee genera occurring across the Arabian Peninsula has been summarized most recently by Dathe (2010) and Engel et al. (2013, 2017). In recent years several genera have been added to the Arabian fauna, including *Melitta* Kirby (Melittidae), Compsomelissa Alfken, and Tarsalia Morawitz (both Apidae) (Algarni et al., 2014; Shebl et al., 2016; Engel et al., 2014, 2017). Prior to the present work, 45 genera of bees have been documented from Saudi Arabia (Engel et al., 2017), and only four panurgines (Borgatomelissa, Meliturgula, Panurginus Nylander, and Panurgus Panzer). None of these previously documented genera are endemic to Arabia (e.g., Patiny and Michez 2007; Michener 2007), and most of these genera are widely distributed across the Palaearctic or even throughout the Old World. Here we record a unique member of the panurgine tribe Melitturgini, representing a genus allied to a group of species largely occurring across Persia and encompassing a variety of morphologies, as documented above. The few known occurrences for the groups discussed herein (Table 1) are loosely analogous to those of species in the genus Tarsalia (Apinae: Tarsaliini) (Engel et al., 2017). The subgenera and species of Tarsalia are distributed across Persia and the Middle East, but also extend into western India and into Central Asia to the East and into Egypt and Sudan in the West. Unfortunately, the biology of this group of bees, comprising the genera Belliturgula, Flavomeliturgula, and Khuzimelissa, remains largely unknown aside from a few floral records. Interestingly, like the new Arabian species described herein, other species where records are available from Iran have also been found at flowers of the thistle subfamily Carduoideae (Asteraceae), and specifically visiting the genera *Centaurea* L. and Carthamus L. (both of tribe Cynareae) (Warncke, 1983). It is possible that all of these

genera are oligolectic on genera of Carduoideae or more generally across Asteraceae. It is greatly hoped that by drawing attention to these unique bees, and the interesting mouthpart specializations found in each (*e.g.*, glossal structure, forms of the labial palpi, premental setation), that efforts will be made to seek out further material in the field, obtain observations on their floral visitation behaviors, locate nests and immatures, and discover the unknown males or females since many of these species are known from a single sex. It is likely such exploration will also uncovered as of yet unknown species, as well as document additional localities from which meaningful distributions can be mapped, ecological niches determined, and broader biogeographic patterns revealed. Naturally, a comprehensive phylogeny of meliturgulines would be of considerable value, but at present the rarity of material (i.e., only one species of the group is known from both sexes and from any substantial number of locality records and specimens) hinders any meaningful study as characters would ideally be drawn from both males and females. Similarly, for DNA sequence data additional collections from the field are necessary. Ultimately, more fieldwork is necessary across the regions in which these bees occur.

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RESEARCH ARTICLE



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

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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 SIMPLEMAPPR (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. http://zoobank.org/7A9537FA-54E1-4E6C-BE9F-7DB8244095B1 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). Punctation 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 punctation (S5 in lateral view more angled and with punctation 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). Punctation 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 tawnycolored (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. Intertegular 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, preapical 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, pitlike 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 intertegular 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, ivorycolored 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. Punctation on basal areas of S2–S5 fine and granulose, distinctly different from coarser punctation 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 female 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 melit-tologist 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, *Acacial 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, *Acacial 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, 13° , 19° , 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, 13° , 19° , 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 fulviventris* 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. fulviventris (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 *Systropha* as the only rophitine genus in Eastern Africa. *Systropha* 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* Lieftinck, 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.

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RESEARCH ARTICLE



Notes on the biology, morphology and generic placement of "Hellwigia" obscura Gravenhorst (Hymenoptera: Ichneumonidae, Ophioninae)

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Abstract

The ophionine ichneumonid known as *Hellwigia obscura* has been reared for the first time, from larvae of *Horisme* sp. (Lepidoptera: Geometridae) feeding on *Clematis vitalba* in The Netherlands. The cocoon and the parasitoid's means of emergence are figured, as are some features of the adult. On a balance of morphological grounds, including some already discussed in the literature, it is proposed that "*Hellwigia*" *obscura* should be excluded from *Hellwigia* and instead be ascribed to the genus *Heinrichiella* stat. rev. as *Heinrichiella obscura* comb. n. Reasons for this change as well as for preferring this generic name to *Protohellwigia* Brues are given

Keywords

Hellwigia elegans, Heinrichiella, Protohellwigia, Horisme, cocoon, emergence, systematics

Introduction

Gravenhorst (1823) erected the genus *Hellwigia* to receive two new nominal species, *H. elegans* Gravenhorst (Fig. 1) and *H. obscura* Gravenhorst (Fig. 2). Holmgren (1859) subsequently fixed *H. elegans* as the type species of the genus *Hellwigia*. Further generic



Figure 1. Hellwigia elegans, female habitus (Cyprus).



Figure 2. Heinrichiella obscura comb. n., female habitus (France).

names introduced for this group were *Diamon* Gistel, 1848 (invalid replacement name for *Hellwigia* Gravenhorst), *Protohellwigia* Brues, 1910 for a new Miocene (or, according to Townes (1966, 1970), perhaps Lower Oligocene) fossil species *P. obsoleta* Brues from the Florissant deposits of Colorado, and *Heinrichiella* Hedwig, 1949 to receive the new nominal species *Heinrichiella monstrosa* Hedwig which was treated by Townes (1966) as a junior synonym of *Hellwigia obscura*. Townes et al. (1965) synonymised both *Protohellwigia* and *Heinrichiella* under *Hellwigia*, though Townes (1970) later stated that the only species certainly included in the genus *Hellwigia* is the type species *H. elegans*. Horstmann (1969,1981) had concluded more emphatically that two genera were involved and placed the nominal *Hellwigia obscura* in the genus *Protohellwigia*, following Townes (1966) who pointed out some shortcomings in the description of Brues (1910) and indicated that *Protohellwigia* was a closer fit to *Hellwigia obscura* than to *Hellwigia elegans*. Townes' (1966) treatment of *Heinrichiella monstrosa* as a junior subjective synonym of *Hellwigia obscura* has been followed by subsequent authors (e.g. Horstmann 1969, 1981, as *Protohellwigia*).

No biological information has been published for any of these taxa, and the main purpose of this paper is to present rearing data, and some limited additional biological information, for the nominal *Hellwigia obscura*. The most appropriate generic name for the species is also considered. The two species described in the genus *Hellwigia* are not only highly divergent from all other Ichneumonidae, but also from each other (Miah 1998). Even though genera are arbitrary human constructs, the issue of whether they should be treated as congeners is sharpened by the assertion that *Hellwigia* per se is a basal member of the Ophioninae (Quicke et al. 2009, Rousse et al. 2016), as the crucial molecular genetic evidence for this was based on the nominal *H. obscura*, not on the type species of the genus, *H. elegans*, which may or may not be closely related.

Methods

Most photographs were taken as single images down one arm of a Wild M5A stereomicroscope with x20 eyepieces using a Canon PowerShot 110. The exceptions (Figs 1, 5) were taken as multiple images by a Canon SLR EOS 5DSR with 65mm macro lens mounted on a copy stand with an automated Z-stepper then stacked using Helicon Focus software version 6.6.1.

Results

Rearing data for the nominal Hellwigia obscura

One of us (JV) collected larvae of *Horisme* spp (Lepidoptera: Geometridae) by beating climbing growth of *Clematis vitalba* at a relatively open calcareous site, Eyserbos, with abundant hedgerows and woodland edge at Eys, Limburg, The Netherlands on 7.ix.2017. Altogether 50 *Horisme* spp larvae were collected, in various stages of growth. Three were easily determined as *H. vitalbata* (Dennis & Schiffermüller) and all produced moths. The remaining 47 comprised both *H. radicaria* (de La Harpe) and *H. tersata* (Dennis and Schiffermüller), but the two species could not be separated in the larval stage and they were reared together. Five of these were parasitized by a gregarious species of Microgastrinae (Braconidae) [the adults escaped but by analogy with rearings from *Horisme* species conducted in England by MRS they were probably *Cotesia nothus* (Marshall)] before becoming fully grown. One succumbed to a species of *Netelia* (*Netelia*) (Ichneumonidae: Tryphoninae) that may be undescribed (Broad and Shaw in prep.), and three prepupae produced banded cocoons that autumn from which adults of the nominal *Hellwigia obscura* emerged during the period 1–7.v.2018 and were passed on to MRS for determination and incorporation into the NMS collection. In addition, five adult *Horisme radicaria* and 33 *Horisme tersata* were reared, the adults of both species emerging between late April and the first half of May 2018. Despite the numerical superiority of *H. tersata* over *H. radicaria* in the host sample from which the specimens were reared, it is unfortunately not yet possible to ascertain which, if not both, of these species serves as host, but it is hoped that this can be pursued in years to come.

The tough cocoon (Fig. 3) is rather stout, ovoid, dark brown with a central paler girdle, and superficially moderately similar to many *Ophion* species except that the girdle is somewhat more raised. The adult emerges in a rather tortuous way that seems quite inefficient: by piercing the cocoon near its capital extremity and cutting a continuous spiral, in the three cases seen of four to six circumferences, to detach a single long, narrow, coiled strip (Fig. 4) to leave a sharply defined terminal opening (Fig. 3) large enough for the adult to emerge.

Generic placement

Horstmann (1969) maintained, and Townes (1970) implied but did not act upon, that the two recent species originally described by Gravenhorst (1823) in the genus *Hellwigia* might best be treated as belonging to separate genera. This is contrary to their present placement both in *Hellwigia* that follows Townes (1970).

At least part of the reason for their still being treated as congeners may stem from the morphological phylogenetic analysis of genera of Campopleginae, which at that time included Hellwigia, conducted by Miah (1998; see also a less explicit account by Miah and Bhuiya 2001). In that analysis the two nominal *Hellwigia* species were scored separately, although most campoplegine genera were scored at the generic level, often following examination of multiple species in the genus. The character set was devised to explore the subfamily Campopleginae, and on that basis it is not surprising that the two Hellwigia species clustered as sisters (based on 12 supposed synapomorphies, but then diverging with 9 autapomorphies for *H. elegans* and 8 for H. obscura). Hellwigia + the highly diverging Skiapus (23 autapomorphies) emerged as a clade based on 18 synapomorphies, with a clade (Hellwigia + Skiapus) + Ophioninae (based on a notional taxon) supported by four synapomorphies. It is admittedly difficult to envisage any other taxon as a sister to either of these highly autapomorphic nominal Hellwigia species but, in our opinion, their purported sister-group relationship was neither adequately tested nor established by the analysis of Miah (1998), as most of the taxa and characters selected for analysis were inappropriate for that purpose and in some cases characters seem to have been incorrectly scored. Further, even if a sister-species relationship were true, the large number of characters by which the two species differ rather far exceeds generic differences currently applied in ichneumonid taxonomy.



Figure 3. Heinrichiella obscura comb. n., vacated cocoon (Netherlands).



Figure 4. Heinrichiella obscura comb. n., spiral cut from apex of cocoon (Netherlands).

Similarities between the species include:

- (i) The highly distinctive distal part of the fore wing venation (Figs 5, 6).
- (ii) The widely exposed, sclerotised and coarsely sculptured labrum (Figs 7, 8).
- (iii) The lack of clear separation between clypeus and face (Figs 7, 8).
- (iv) Ovipositor structure (Figs 1, 2).



Figure 5. Hellwigia elegans, wings (Cyprus).



Figure 6. Heinrichiella obscura comb. n., wings (Netherlands) [combined from two images].

Differences, probably including both autapomorphies and plesiomorphies (unassessed here) judged to be important by Horstmann (1969), restated or expanded, are:

- (i) The antenna with terminal segments greatly broadening to make the antenna very strongly clubbed in *H. elegans* (true of both sexes but particularly pronounced in the male, Fig. 9) but unmodified in nominal *H. obscura* (in the male, Fig. 10, flagellar segments are just very slightly broadened post-centrally but then the antenna slightly attenuates apically).
- (ii) A genal bridge closing the ventral hypostomal space of *H. obscura* but absent in *H. elegans* (this difference is illustrated by Horstmann 1969: Figs 1, 2). Miah (1998)



Figure 7. Hellwigia elegans, mandibles, labrum, clypeus (Turkey).



Figure 8. Heinrichiella obscura comb. n., mandibles, labrum, clypeus (Netherlands).



Figure 9. Hellwigia elegans, male antenna (Israel).



Figure 10. Heinrichiella obscura comb. n., apical half of male antenna (Netherlands).

scores the junction of the hypostomal and genal carinae far distant from the mandible in *H. obscura* as a separate autapomorphy.

- (iii) The epicnemial carina borders the anterior of the mesosternum in an unbroken straight line in *H. elegans*, while it is centrally produced to form a projection towards the space between the fore coxae in *H.obscura*.
- (iv) The apically flared hind leg tarsomeres of *H. elegans*, unmodified in *H. obscura*.
- (v) The sclerotised part of sternite I of the metasoma reaching only to the anterior end of the postpetiole (i.e. level with the spiracles) in *H. elegans* but beyond the middle of the postpetiole (i.e. well past the spiracles) in *H. obscura*.
- (vi) The hypandrium (male subgenital plate) which is greatly expanded and ventrally flat (also bearing strong spines) in *H. elegans* (Fig. 11), but unmodified (small, with a v-shaped cross section as in the preceding sternite, and lacking spines) in *H. obscura* (Fig. 12).



Figure 11. Hellwigia elegans, apex of male metasoma (Turkey).



Figure 12. Heinrichiella obscura comb. n., apex of male metasoma (Netherlands).

On these grounds Horstmann (1969) placed the two species in different genera, as *Hellwigia elegans* and *Protohellwigia obscura*. Additional characters, including those given by Miah (1998), to support the generic separation are:

(vii) The mandibles are bidentate with a fairly slender elongate upper tooth and a much shorter lower one in *H. elegans* (Fig. 7) but almost quadridentate with the upper tooth bearing a produced flange below, somewhat like some *Ophion* species, and the lower tooth clearly divided in *H. obscura* (Fig. 8). This difference seems not to have been previously noted.

- (viii) The claws, which are untoothed in both taxa, are evenly curved in *H. elegans* (Fig. 13) but bent at right angles in *H. obscura* (Fig. 14) (Miah 1998). Gauld (1985) regarded a sinuous pectinal comb on tarsal claws as an autapomorphy for Ophioninae.
- (ix) The lack of a spurious vein extending distally close to the wing margin from the posterodistal corner of the first subdiscal cell in *H. elegans* (Fig. 5) but its presence in *H. obscura* (Figs 6, 15). The presence of this vein has been regarded as a strong autapomorphy for Ophioninae (cf. Gauld 1985, Broad et al. 2018), and the difference between the two species seems not to have been previously noted.
- (x) The lack of basal hamuli in *H. elegans* (Fig. 5), but their presence in *H. obscura* (Fig. 6) (Miah 1998).

Many of the features in which the two species differ are illustrated but without comment by Choi et al. (2011).

Despite the difficulty of associating either of the nominal *Hellwigia* species with any other taxon, we assert that the very wide morphological separation between them are strong grounds for us to assign the nominal *Hellwigia obscura* to a different genus. It differs from the fossil *Protohellwigia obsoleta* in wing venation (figured by Brues (1910), although Townes (1966) states that the venation in the area of the pterostigma of *P. obsoleta* had been misinterpreted and is closer to that of the nominal *Hellwigia obscura* (e.g. mandible, claws, hypostomal bridge) were simply not visible for assessment in the fossils. On balance it seems inappropriate to place the nominal *Hellwigia obscura* in *Protohellwigia* Brues even though Horstmann (1969, 1981) did so. An alternative and more clearly suitable generic name is already in existence: *Heinrichiella* Hedwig, 1949 (nec Tereshkin 2000) has its type species widely considered to be a subjective junior synonym of the nominal *Hellwigia obscura*, and it is logical therefore to resurrect as a valid genus *Heinrichiella* stat. rev. and transfer this species to become *Heinrichiella obscura* (Gravenhorst), comb. n.



Figure 13. Hellwigia elegans, hind claw (Israel).



Figure 14. Heinrichiella obscura comb. n., hind claw (Netherlands).



Figure 15. Heinrichiella obscura comb. n., part of fore wing with spurious vein (France).

Discussion

Biology

The way in which the adult *Heinrichiella obscura* comb. n. leaves its cocoon differs markedly from the emergence habits seen in European species of *Ophion* (a chewed hole involving the removal of many irregular bits) and *Enicospilus* (a neatly detached cap). Although not directly observed, the unusual means of eclosion of adult *Heinrichiella obscura* comb. n. must relate closely to the structure of its mandibles. In a few groups of Ichneumonidae (e.g. Diplazontinae, and the genus *Banchus* (Banchinae), cf. Broad et al. 2018) the upper tooth is similarly divided and the mandibles are used to

cut successive short strips from the cocoon (or host puparium in the case of Diplazontinae) as the adult emerges. In all 48 vacated cocoons of *Banchus* in the NMS collection, comprising four species, an oval emergence hole just below the cocoon apex had clearly been made by detaching successive short strips. Rotheray (1981) records and diagrammatically figures the cutting of a succession of discrete semi-circular strips of the syrphid host's puparium by the emerging adult diplazontine *Diplazon pectoratorius* (Thunberg), remarking that the outcome was similar in 12 other diplazontine species he had under less intensive observation. However, the cutting of a single continuous concentrically circular strip from the cocoon in the process of adult eclosion seen in *Heinrichiella obscura* comb. n. is, as far as we are aware, not recorded elsewhere in the Ichneumonidae. It seems probable that the divided lower tooth of *Heinrichiella obscura* comb. n., absent in both *Banchus* and Diplazoninae, may play an important part in this.

A series of female *Heinrichiella obscura* comb. n. in NMS collected by Malaise trap in France (Dordogne) by RR Askew in September (two in the period 1–21.ix.1999 and one 16–30.ix.2000), in conjunction with the present rearings in May, suggests that, like its *Horisme* hosts, *H. obscura* is at least bivoltine, and the late dates also indicate that it probably attacks final instar host larvae, as appears to be typical for European Ophioninae (cf. Broad et al. 2015).

Given the suggested basal position within Ophioninae of *Heinrichiella obscura* comb. n. (see below) it is of some significance that its host is a geometrid, a host group that may be ancestral for Ophioninae given also that it is used by a few species of apparently relatively basal *Ophion* in Europe (Schwarzfeld et al. 2015), although many species of both the putatively more derived *Ophion*- and *Enicospilus*-groups are, as far as is known, particularly associated with Noctuoidea (see also Rousse et al. 2016).

Commentary on the higher classification of Hellwigia sensu Gravenhorst

Although Townes (1970) continued his earlier (Townes et al. 1965) treatment of *Hell-wigia* s. l. + *Skiapus* as an isolated tribe Hellwigiini within Campopleginae, Horstmann (1969) had recognised the distinctiveness of *Hellwigia* sensu Gravenhorst (1823) plus Brues'(1910) fossil taxon *Protohellwigia*, and proposed subfamily status for the group as Hellwigiinae (he did not consider *Skiapus*). More recent work, depending heavily on molecular genetics, but engaging also Miah's (1998) morphological study of Campopleginae s. l., has placed "*Hellwigia*" within the Ophioninae (Quicke et al. 2005; see also Belshaw and Quicke 2002) with the eventual conclusion that it represents a basal lineage of that subfamily, but without an identifiable tribal placement (Quicke et al. 2009, Rousse et al. 2016). However, the representative of "*Hellwigia*" on which these 21st century molecular genetic analyses were entirely based was not the type species *Hellwigia elegans* (Fig. 1) but rather the much more superficially and structurally ophionine-like *Heinrichiella obscura* comb. n. (Fig. 2), which also appears (Quicke et al. 2005, 2009) to be the sole "*Hellwigia*" in the morphological analysis. That, then,

is the putatively basal ophionine, leaving the interesting phylogenetic position of the more autapomorphic *Hellwigia elegans* open as, apart from considerable similarities in wing venation (Figs 5, 6, 15; but note the perhaps telling absence of the fore wing spurious vein in *H. elegans* and its lack of basal hamuli in the hind wing, as well as differences in vein 1cu-a), there seems little to strongly support their being very closely related—though future work may demonstrate that they are. For now, though, there is good reason to isolate the species believed to be a basal ophionine from the name *Hellwigia*.

It would, of course, be extremely interesting to discover the host of *Hellwigia elegans* (apart from capture data, nothing is known of its biology beyond its ovipositor structure (Fig. 1) suggesting that it should be a koinobiont endoparasitoid), but the probably easier exercise of investigating its phylogenetic position via molecular genetics will be more crucial for clarifying whether or not it, like *Heinrichiella obscura* comb. n., can be considered to be a basal ophionine.

It is relevant to point out that the caption for Fig. 14c in Quicke et al. (2009), showing the venom gland and reservoir intima, refers to *Hellwigia elegans*, but this is almost certainly a lapsus for *H. obscura*, because (i) the French female specimen (cited in appendices) loaned from the National Museums of Scotland (NMS) collection for DNA was returned with most of the metasoma snipped off, (ii) there is otherwise no mention of *H. elegans*, including in the lists of material examined, in the above interconnected series of 21st century papers, and (iii) the female specimens in the Natural History Museum, London, where the work was partly based, have intact metasomas.

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