

Superparasitism of *Eoxenos laboulbenei* De Peyerimhoff (Strepsiptera: Mengenillidae) by *Idiomacromerus gregarius* (Silvestri) (Hymenoptera: Chalcidoidea) in southern Spain

Juan A. Delgado^a, Richard R. Askew^b, Francisco Collantes^a and Jeyaraney Kathirithamby^c*

^aDepartamento de Zoologia, Facultad de Biologia, Universidad de Murcia, Murcia, Spain; ^bLe Bourg, St Marcel du Périgord, Ste Alvère, France; ^cDepartment of Zoology, University of Oxford, Oxford, UK

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A female puparium of *Eoxenos laboulbenei* De Peyerimhoff (Strepsiptera: Insecta) found in Mula, Murcia, Spain was parasitized by five larvae of *Idiomacromerus gregarius* (Silvestri) (Hymenoptera: Chalcidoidea: Torymidae). The parasitized puparium was kept in the laboratory until the following summer, when four *I. gregarius* adults emerged from it. This species of chalcidoid is rarely found. It was first described in 1943 from Italy by Silvestri and the present report is the first record from Spain. Here we re-examine and redescribe the newly discovered specimens of *I. gregarius*, add further details about its morphology and give a brief account of its biology including a new record (the mengenillid *E. laboulbenei*).

Keywords: Torymidae; parasitoid; Strepsiptera

Introduction

The primitive family Mengenillidae of the entomophagous insect parasitoid order Strepsiptera are parasitoids of Zygentoma (Thysanura) (Carpentier 1939; Silvestri 1941). Both males and females of the family Mengenillidae emerge from the host to pupate externally, unlike in the derived sister group Stylopidia, where females remain permanently in the host even as neotenic adults and the males pupate in the host and emerge as free-living adults. Strepsiptera exhibit extreme sexual dimorphism, especially in the suborder Stylopidia where females are "larviform" with no external adult characters (Kinzelbach 1971; Kathirithamby 1989, 2009). The Mengenillidae consists of three genera, *Eoxenos, Mengenilla* and *Congoxenos*, the first two genera parasitize apterygote hosts (the host of *Congoxenos* is not known) whereas Stylopidia parasitize pterygote hosts (Kathirithamby 2009; McMahon et al. 2011). There is only one species of *Eoxenos* (*Eoxenos laboulbenei*), which that has been recorded from the following countries: Algeria, Cyprus, Egypt, France, Greece, Israel, Italy, Lebanon, Libya, Malta, Morocco, Spain, Syria, Tunisia and Turkey. It has been recorded that E. laboulbenei parasitizes Tricholepsima aurea (Dufour), Neoasterolepisma crassipes (Escherich) and *Neoasterolepisma wasmanni* (Moniez) (Silvestri 1941).

^{*}Corresponding author. Email: jeyaraney.kathirithamby@zoo.ox.ac.uk

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Eoxenos laboulbenei De Peyerimhoff was found close to Mula, Murcia, southern Spain parasitizing *Neoasterolepisma pallida* Molero, Gaju and Bach, (Zygentoma). Larvae of both sexes of *E. laboulbenei* emerge from their thysanuran host to pupate under stones and tree bark. Both nymphs and adults of stylopized Zygentoma have been found in nests of harvester ants and female pupae of *E. laboulbenei* can be found outside ants' nests (Kathirithamby, Delgado and Collantes, unpublished data). The last larval instars of the male and female emerge from the host, and their cuticle tans to form a tough puparium within which they pupate (Figure 1). The male and female puparium and neotenic female adults of Mengenillidae have eyes, antennae, mouthparts and legs, but are wingless, and males emerge as free-living adults (De Peyerimhoff 1919; Bolivar y Pieltain 1926; Hofeneder 1910; Parker and Smith 1933, 1934; Silvestri 1941, 1943).

Ants, silverfish and strepsipterans interact in a multitrophic food web, which might be an indication of the manner in which invertebrates have adapted to the extreme arid conditions of this area. Here we report the first record from southern Spain of a further member of this trophic food web, the little known hymenopteran parasitoid wasp *Idiomacromerus gregarius* (Silvestri) (Hymenoptera), which is a parasitoid of the pupae of both male and female *E. laboulbenei*.

It is 70 years since Silvestri's (1943) pioneering study of Mengenillidae in which I. gregarius is described as a parasitoid, but since then I. gregarius has scarcely been mentioned in the literature. Silvestri (1943), however, was able to collect a large number of specimens of *I. gregarius* and he gave descriptions of the immature stages with detailed observations on aspects of the biology, stating that it was a parasitoid of Mengenilla, another mengenillid genus, and naming Mengenilla quaesita (Silvestri), Mengenilla subnigrescens (Silvestri) and Mengenilla spinulosa (Silvestri), in mainland Italy, and Mengenilla parvula (Silvestri) in Sicily, as its hosts. Mengenilla quaesita, M. subnigrescens and M. spinulosa are now regarded as junior synonyms of Mengenilla chobauti Hofeneder 1910 (Kinzelbach 1971) and have been listed as parasites of Lepismatidae (Zygentoma) occurring in the Mediterranean region of Europe and northern Africa, as far south as Sudan and as far north as the Atlantic coast of Iberia and the English Channel coast of France, and in the Middle East. This reported wide range of M. chobauti, however, suggests that it may be a complex of cryptic species, the presence of which can only be confirmed by molecular characterization, as was the case for the Nearctic/Neotropical Myrmecolacidae strepsipteran Caenocholax fenyesi Pierce sensu lato, study of which showed the existence of at least 10 cryptic lineages consistent with separate species (Hayward et al. 2011). Silvestri (1941), in his description of *E. laboulbenei*, mentions that *I. gregarius* is a parasite but no details are given as he did with the *Mengenilla* species in 1943. Luna de Carvalho (1950) found a female puparium of *E. laboulbenei* in Portugal with three larvae, and suggested that they could have been the hymenopteran parasitoid, Orthochalcis mengenillarum Silvestri. Luna de Carvalho (1953) however, states that when the above larvae had become adults it was verified that they were *I. gregarius*. Noves (2012) gives I. gregarius as a parasite of E. laboulbenei in Portugal, as does Herting (1973); both records perhaps taken from Luna de Carvalho (1953).

A female puparium of *E. laboulbenei* was found under bark near Mula, Murcia, Spain, on 2 September 2011. The puparium had a broken anterior end (head and prothorax) and contained five fully grown chalcidoid larvae (Figure 1B, E) but there was no trace of the pupa or neotenic adult of *E. laboulbenei* inside the puparium. We



can only conclude that the larvae had consumed the female *E. laboulbenei* pupa before our collection. The material was kept in the laboratory at ambient temperature. No activity was observed during the winter of 2011, but in the spring of 2012 it was noted that the larvae had pupated and 2 days before eclosion some movement of the antennae and legs of the pharate adult parasitoids inside their pupae was observed (Figure 1C). On 14 June 2012, 1 male and 3 female chalcid adults emerged from the puparium (Figure 1D) through a hole on the ventral surface of the puparium (Figure 1F). One larva was missing and it is assumed this was due to cannibalism by the other larvae.

At the same time as the puparium was collected, another *E. laboulbenei* female puparium was found that was empty with no pupa or neotenic adult inside. On the ventral surface of this puparium there was a hole approximately the same size as that of the parasitized puparium, suggesting that it might have also been parasitized by the same chalcidoid species. Silvestri (1943) states that these wasps have two generations a year. Therefore the empty puparium might have been parasitized by the first generation.

The adult parasitoids that emerged from the female puparium of *E. laboulbenei* closely match the original description of *Lochites gregarius* Silvestri (Silvestri 1943). The location of the type of *L. gregarius* (which is now placed in the genus *Idiomacromerus*) is not known and hence the holotype material could not be examined (Grissell 1995). It is evidently a little known species, and we provide here details of the Spanish material collected supplementing Silvestri's (1943) description of the specimens from Italy.

Description

Female (Figures 2, 3). Head and mesosoma metallic green with a few bronze reflections especially on axillae and propodeum. Metasoma brown with very weak metallic reflections on posterior half, first and second metasomal segments yellow-brown, tergites of segments 3–5 each with a large yellowish area laterally. Antenna with yellow scape, pedicel mostly yellow but dorsal surface darker and faintly metallic, flagellum dark brown. Metacoxae dark green with bronze reflections, otherwise yellow apart from brownish fifth tarsal segments and claws. Wings hyaline with light brown venation; tegulae yellow. Body length (excluding ovipositor) 1.7 mm, ovipositor sheath 0.7 mm.

Head in anterior view (Figure 3C) $1.2 \times as$ broad as high; eyes separated by $1.3 \times$ their height; genae straight, strongly convergent; malar space about $0.4 \times$ height of eye; face with short, white setae. Head in dorsal view (Figures 2A, 3B) rather more than $2 \times as$ broad as long; occipital carina absent. Antenna (Figure 3A–C, H) 11173;

Figure 1. (A) Free-living puparium of female *Eoxenos laboulbenei* containing a neotenic adult (arrow). (B) Free-living puparium of female *Eoxenos laboulbenei* with fully grown larvae of *Idiomacromerus gregarius* (arrow). (C) Free-living puparium of female *Eoxenos laboulbenei* with pupae of *Idiomacromerus gregarius* one day before hatching (arrow). (D) Empty puparium of female *Eoxenos laboulbenei* after the hatching and emergence of *Idiomacromerus gregarius* (arrow). (E) Detail of larvae of *Idiomacromerus gregarius* from (B). (F) Puparium of female *Eoxenos laboulbenei* with chalcid exit hole.



Figure 2. Female Idiomacromerus gregarius. Habitus. (A) Dorsal view. (B) Lateral view.



Figure 3. *Idiomacromerus gregarius*, female. (A) Head, lateral view. (B) Head, dorsal view. (C) Head, frontal view. (D) Mesosoma, dorsal view. (E) Mesosoma, lateral view. (F) Forewing, dorsal view. (G) Detail of forewing showing stigma and uncus. (H) Antenna, lateral view. (I) Mesotarsomeres and tibial apex.

flagellum with anellus transverse, about twice as broad as long; second flagellar segment intermediate in size between anellus and third flagellar segment, considered as the first funicle segment (F1) of seven because it is about $1.5 \times$ as long as and $1.5 \times$ broader than the anellus and it bears sensilla; F2 subquadrate, broader than and about $1.3 \times$ as long as F1; F3 broader than F2, F3–F7 more or less transverse, F7 about $1.3 \times$ as broad as long and $1.3 \times$ as broad as F3; clava $2.4 \times$ as long as broad, slightly broader than F7, without an apical spine; sensilla in a single transverse row on each funicle and claval segment.

Mesosoma in dorsal view (Figure 3D) $1.5 \times$ as long as broad; mesoscutum rather dull with very fine, irregular sculpture in which small, shallow punctures are difficult to discern except posteriorly where they are separated on average by about three diameters; scutellum with sculpture less deeply engraved with punctures more distinct and more widely separated. Posterior quarter of the scutellum with coarser sculpture, more shiny, but not sharply differentiated and frenal line absent. Metapleuron (Figure 3E) with anterior (dorsal) margin straight. Propodeum about one-third the length of scutellum, shiny with very weak reticulate sculpture, strongest in shallow spiracular sulci, separated from metanotum by a narrow transverse groove divided into a few foveae by about six short, longitudinal carinae; median carina virtually absent; spiracles of moderate size, separated from metanotum by approximately the lesser diameter of the (ovoid) spiracle. Mesotibia with apical spur not quite half as long as mesobasitarsus (Figure3I); metacoxa with dorsal surface pilose; metafemur relatively slim, $5 \times as$ long as deep and broadest medially, its ventral surface smooth; metatibia with two relatively short apical spurs, the longer, inner spur hardly as long as apical width of tibia and only $0.35 \times \text{length of metabasitarsus}$.

Forewing (Figure 3F) lengths of costal cell: marginal vein; stigmal vein: postmarginal vein as 70 : 42 : 10 : 19; stigmal vein (Figure 3G) forming an acute angle to post-marginal vein, its stem gradually expanding into a long stigma; stigma fully twice as long as broad, separated from lower edge of postmarginal vein by little more than its depth, uncus about as long as depth of stigma; costal cell upper surface with a row of marginal hairs in distal two-thirds, plus one to three hairs near apex of cell, under surface with marginal hair row almost complete, although sparse proximally, and with scattered hairs in distal one-third of cell; basal vein pilose; basal cell with a very few hairs on upper surface near apex, closed below by a proximally sparse row of hairs on cubital vein; speculum on upper surface extending to middle of marginal vein but anteriorly partly effaced by hairs on under surface, open below.

Metasoma (Figures 2A, B, 3A) excluding ovipositor sheath $1.3 \times as$ long as mesosoma; anterior tergites with posterior margins not medially emarginated, apex of hypogium at $0.4 \times gaster length$. Ovipositor sheath upward sloping, $0.55 \times as$ long as metasoma and $1.3 \times as$ long as metatibia.

Male (Figure 4). Mesosoma green, brighter than female with bronze reflections almost restricted to propodeum; legs yellow with middle and hind femora faintly brown medially; gaster dorsally with a large sub-basal yellow spot, otherwise brown to dark brown with weak metallic reflections. Body length 1.3 mm.

Eyes not reduced (Figure 4B). Antenna (Figure 4C) 11263; scape $4.3 \times$ as long as broad, rather broader than in female, fusiform; first and second flagellar segments anelliform, transverse, much shorter than quadrate third flagellar segment (F1); F2 to F6 more or less transverse; setae on flagellum somewhat longer than in female. Scutellum with posterior quarter extremely weakly sculptured, shiny, with a few



Figure 4. *Idiomacromerus gregarius*, male. (A) Habitus, lateral view. (B) Head, frontal view. (C) Antenna, lateral view. (D) Aedeagus, ventral view.

widely separated punctures, marked off from anterior, darkish green part of scutellum by a transverse blue-green line. Aedeagus as in Figure4D.

The above specimens agree with the description and accompanying figures of *L. gregarius* by Silvestri (1943) from Italy with two differences:

i. The ovipositor sheath is described by Silvestri as $0.67 \times$ the length of the metasoma (= gaster) and in Silvestri's figure (Silvestri 1943, fig. XXII) it is shown as $0.61 \times$ the length of the metasoma, the discrepancy accounted for by the upward inclination of the ovipositor sheath. The female we examined here has an ovipositor sheath $0.55 \times$ the length of the metasoma.

ii. The median carina on the propodeum which is scarcely visible in the specimens we examined appears as a fine but distinct line in Silvestri (1943, fig. XXII).

Material examined One male, three female adults of *I. gregarius* that emerged on 14 September 2012 from a female puparium of *Eoxenos laboulbenei* De Peyerimhoff (Strepsiptera: Mengenillidae), collected from beneath bark near Mula, Murcia, Spain on 2 September 2011.

Voucher specimens

Idiomacromerus gregarius 14 June 2012. three females, one male. Farm and lemon orchards on the road from Mula to Pliego, Murcia, 38°00′25.27″ N, 2°28′52.46″ W, Spain. Museum of Natural History, Oxford (Delgado and Collantes).

Generic attribution

Lochites Förster, 1856 is preoccupied by Lochites Gistl, 1848 in Protozoa, and the next available name for the hymenopteran genus is *Idiomacromerus* Crawford, 1914. Grissell (1995) proposed the new combination Idiomacromerus gregarius (Silvestri 1943). Idiomacromerus belongs to the tribe Microdontomerini (Torymidae: Microdontomerinae), which includes genera whose separation is complex, difficult and sometimes uncertain Grissell (1995: 84) writes "There is no doubt that Microdontomerus, Idiomacromerus, and Adontomerus are extremely closely related". Following Grissell's own key to genera of Microdontomerinae, I. gregarius runs to Microdontomerus Crawford, 1907 by virtue of the female antennal flagellum having seven funicle segments and a single anellus. The apparent absence of any medial emargination of the basal gastral tergites, however, is suggestive more of Idiomacromerus than Microdontomerus. The metafemur is unarmed and unusually slim, about five times as long as broad, differing from other species in either genus. Idiomacromerus gregarius does not fit comfortably into either Idiomacromerus or Microdontomerus, but it seems preferable to retain it in Idiomacromerus pending a re-evaluation, supported by molecular analysis, of generic limits in Microdontomerini.

Biology

Together with *I. gregarius*, three species of Chalcidoidea, *Hockeria mengenillarum* (Silvestri) (Chalcididae), *Dibrachys microgastri* (Bouché) (Pteromalidae) and *Merostenus* sp. (Eupelmidae) are listed by Noyes (2012) as parasitoids of Mengenillidae (*Eoxenos* and *Mengenilla*). *Dibrachys microgastri* (syn. *Dibrachys cavus* [Walker]) is a polyphagous species with an exceedingly long recorded host list and is a secondary parasitoid of Lepidoptera, cocoons of Ichneumonoidea (Hymenoptera) and puparia of Tachinidae (Diptera). The superficial resemblance of these to the free-living puparium of Mengenillidae has perhaps facilitated the inclusion of *Mengenilla* in the host range of *D. microgastri*. In contrast, *I. gregarius* and *H. mengenillarum* appear to be host-specialized parasitoids, in all

probability limited to only parasitizing the strepsipteran family Mengenillidae. Our record here from Spain is a new country record.

Silvestri (1943) states that both the male and female pupari are parasitized. *Idiomacromerus gregarius* females either drill through the hard wall of the puparium wall, or insert the ovipositor through the broken anterior region of the head and prothorax of the puparium and deposit a number of eggs on the surface of the male or female pupa, neotenic female, or male subimago inside the puparium. The developing parasitoid larvae feed and consume the body of the host female pupa, neotenic female or male subimago *Eoxenos* sheltered within the hard puparium. They then pupate within the puparium (Figure 1B, E) (which is now empty of all host remains) eventually emerging as adults through the exit hole that they make in the surface of the puparium (Figure 1C, D, F). The number of *I. gregarius* that develop in one host varies between three and seven individuals (Silvestri 1943). Both males and females are represented in a single brood, as recorded here, and by Silvestri (1943). Such gregarious development is exceptional in Microdontomerini.

Preparation of figures

Specimens were prepared for study with the help of a Leica MZ9S stereomicroscope. Habitus photographs were taken with the help of a Nikon eclipse E600 microscope equipped with a Nikon DS-U2 unit Camera and following the suggestions proposed by Buffington et al. (2005). For each illustration a series of photographs were taken at various focal layers and then stacked using the "do stack" function or "pyramid weighted average" function of CombineZP software (Hadley 2010). Some images were subsequently edited and made symmetrical digitally.

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