

A REVIEW OF THE IBEROBALERIC AND MACARONESIAN SPECIES OF *EUPELMUS (MACRONEURA)* WALKER, 1837 (HYMENOPTERA, CHALCIDOIDEA, EUPELMIDAE)

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ABSTRACT

A revised checklist of eight of the twelve known palaearctic species in the subgenus *Macroneura* of *Eupelmus* occurring in the Iberian Peninsula, Balearic and Macaronesian islands (Azores, Balearics, Canaries, Madeira) is presented. Records of the distribution in the region of all the revised species are given with new biological notes, including host insects and plants. *Eupelmus (Macroneura) seculatus* is a new record for the Canary Islands and *Eupelmus (Macroneura) vesicularis* is recorded for the first time in Portugal. Additionally, a study of Malaise trap captures of species of *Macroneura* in an arid habitat in south-east Spain is presented and discussed. 358 individuals belonging to six species were collected and identified. *Eupelmus (Macroneura) muellneri* comprised 43.5% of the *Macroneura* and was the most abundant species followed by *E. (M.) barai* (25.4%).

Keywords: eupelmids; parasitoids; gall wasps; Spain; Portugal; Azores; Canary Islands; Madeira; Almería; Malaise trap.

RESUMEN

Revisión de las especies de *Eupelmus (Macroneura)* Walker, 1837 del ámbito iberobalnear y Macaronesia (Hymenoptera, Chalcidoidea, Eupelmidae)

Se presenta la revisión y una lista anotada de ocho de las doce especies paleárticas de *Eupelmus (Macroneura)* que se conocen de la Península Ibérica, Islas Baleares y Macaronesia (Canarias, Madeira y Azores). Se aportan para cada especie las citas en cada ámbito geográfico, incluyendo nuevos datos biológicos, como los de sus insectos y plantas hospedadoras. *Eupelmus (Macroneura) seculatus* es nueva cita para las Islas Canarias y *Eupelmus (Macroneura) vesicularis* se cita por primera vez de Portugal. Como complemento a esta revisión, se presentan los resultados de las capturas de especies de *Macroneura* efectuadas con una trampa Malaise que se mantuvo operativa en primavera y verano de 2013 en una zona árida del sureste español (Mojácar, Almería). Se capturaron 358 ejemplares de seis especies, siendo *Eupelmus (Macroneura) muellneri* (43,5% del total) la especie más abundante en las muestras, seguida de *E. (M.) barai* (25,4%).

Palabras clave: eupelmidos; parasitoides; avispas de las agallas; España; Portugal; Azores; Islas Canarias; Madeira; Almería; trampa Malaise.

Recibido/Received: 12/05/2020; **Aceptado/Accepted:** 16/07/2020; **Publicado en línea/Published online:** 18/02/2021

Cómo citar este artículo/Citation: Askew, R. R., Rey del Castillo, C., Rodríguez Rojo, M. P. & Nieves-Aldrey, J. L. 2021. A review of the Iberobaleric and Macaronesian species of *Eupelmus (Macroneura)* Walker, 1837 (Hymenoptera, Chalcidoidea, Eupelmidae). *Graellsia*, 77(1): e119. <https://doi.org/10.3989/graellsia.2021.v77.281>

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Introduction

A recent study (Fusu, 2017) of European species in the subgenus *Macroneura* Walker, 1837 of *Eupelmus* Dalman, 1820 (Hymenoptera: Eupelmidae) based upon both molecular and morphological analyses, revealed the existence of twelve species including four which had hitherto been confused within the *E. (M.) vesicularis* aggregate. In an annotated checklist of the Eupelmidae of Iberia and the Canary Islands (Askew & Nieves-Aldrey, 2017), we indicated our intention of preparing, after publication of Fusu's paper, an updated account of subgenus *Macroneura*. We present this here, recognising the presence in the studied geographic area of eight species of *Eupelmus* (*Macroneura*), three of which are in the *vesicularis* complex.

Material and Methods

Examined materials included dry mounted specimens as preserved in ethanol. The revised material comes from three sources: 1/ Materials from R.R. Askew collection (259 specimens); 2/ Materials from J. L. Nieves-Aldrey collection, and other eupelmid materials deposited in the general collection of the Museo Nacional de Ciencias Naturales (Madrid, Spain) (MNCN), the latter included samples collected by historical Spanish hymenopterists: Cándido Bolívar y Pieltáin, Gonzalo Ceballos y Fernández de Córdoba, José María García Mercet and others.; 3/ Eupelmid materials collected in a Malaise trap sampling programme conducted by Carmen Rey in an arid habitat in south-east Spain (358 specimens).

A single Malaise trap of American-design (Townes, 1972; Nieves-Aldrey & Rey del Castillo, 1991) was

installed in the site at La Parata near Mojácar, Almería ($37^{\circ} 07' 14,9''$ N, $01^{\circ} 51' 00,6''$ W) and was operated from 5 May until 28 August, 2013. Samples were collected weekly and stored in 75% ethanol.

The trap was situated in a 'barranco' or gorge close to the Mediterranean Sea (Fig. 1). Lithologically the area consists of sand stone and marls at the bottom of the gorge and black slate on the northern slopes. The flora of the slopes of the barranco includes species of *Anthyllis*, *Ulex*, *Osyris*, *Retama*, *Ephedra*, *Artemisia*, *Genista*, *Thymelaea*, *Phlomis*, *Chamaerops*, *Lavandula*, *Carthamus* and *Inula*, whilst small trees of *Ceratonia siliqua*, *Pistacia lentiscus* and *Acacia retinoides* grow at the bottom. The grasses *Stipa* and *Hyparrhenia* are abundant on abandoned terraces together with old plantations of *Opuntia ficus-indica*.

Colour photographs of habitus of adult *Macroneura* species were taken by JLNA with a Nikon digital camera attached to a Leica light microscope.

Results

ANNOTATED CHECKLIST OF *EUPELMUS (MACRONEURA)* FROM THE IBERIAN PENINSULA, BALEARIC AND MACARONESIAN ISLANDS

Eupelmus (Macroneura) aseculatus (Kalina, 1981) (Fig. 2A)

The male of this species has not been identified and may not exist (Fusu, 2017). Previous rearing records in the region are from galls of the Cynipidae (Hymenoptera: Cynipoidea) *Aylax papaveris* (Periss) on *Papaver* in Madrid (1987, JLN-A) (Askew & Nieves-Aldrey, 2000 as 'E. sp. indet. B'; Askew et al., 2006), *Andricus quercusradicis* (Fabricius)

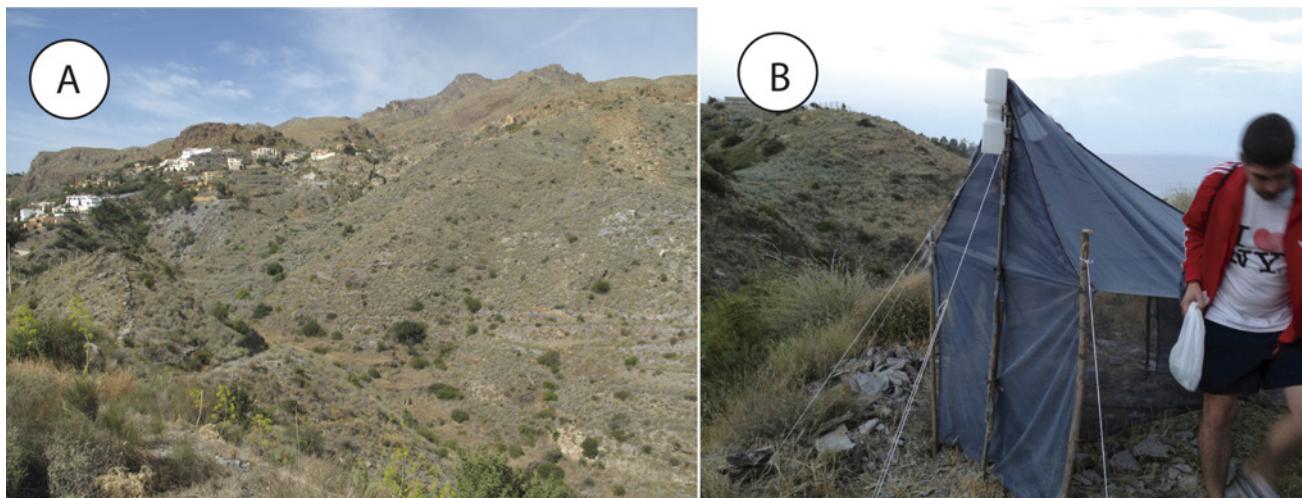


Fig. 1.— Collecting site of La Parata (Mojácar, Almería, Spain) where a Malaise trap was operating in 2013: (A) General habitat aspect. (B) Malaise trap used.

Fig. 1.— Lugar de muestreo en La Parata (Mojácar, Almería) donde se instaló una trampa Malaise para la captura de insectos en 2013: (A) aspecto general del hábitat. (B) Trampa Malaise utilizada.

on *Quercus* sp. in Madrid (1983, JLN-A) and two species of *Callirhytis*, *C. glandium* (Giraud) and *C. rufescens* (Mayr), on *Quercus suber* in Salamanca (1982, JLN-A) and Toledo (1989, JLN-A) (Askew & Nieves-Aldrey, 2000, 2017; Fusu, 2017). Fusu (2017) gives Granada (1973, Z. Bouček) as an additional locality, and further specimens have been found in the Malaise trap samples from La Parata (Almería, Mojácar) (Table 1).

Eupelmus (Macroneura) falcatus (Nikol'skaya, 1952)

Eupelmus (M.) falcatus is predominantly, perhaps exclusively, a parasitoid in stems of herbaceous plants and particularly grasses in which it attacks species of *Tetramesa* (Eurytomidae) or their chalcidoid parasitoids. It appears to be rather uncommon in Iberia with records limited to Madrid and Lleida, and only one addition to our previously quoted records (Askew & Nieves-Aldrey, 2000, 2017): 1♀ reared from a stem of *Stipa parviflora* (Lleida, 2008, A. Ribes) (Fusu, 2017). It was not found in the Malaise trap samples from La Parata (Table 1).

Eupelmus (Macroneura) maculatus (Ferrière, 1954)

There do not appear to be any host records for this rather rare species which has a Mediterranean distribution in Europe. First recorded in the Iberian Peninsula in Spain from Barcelona in Askew & Nieves-Aldrey (2000) (1♀ 1974, Z. Bouček), an additional 12♀ from presumably the same collection are cited by Fusu (2017: 83) as well as 2♀ collected vi.1971 at Calella de Costa, Barcelona by Bouček. In addition, Fusu reports specimens collected by Bouček in 1973 in Alicante (2♀), Granada (1♀) and Malaga (1♀). The La Parata (Almería) Malaise trap samples (Table 1) included only a single female which was previously reported by Askew & Nieves-Aldrey (2017).

Eupelmus (Macroneura) muellneri (Ruschka, 1921) (Fig. 2B)

Eupelmus (M.) muellneri has a Mediterranean distribution and is common in Spain and present also in Portugal and the Balearic (Majorca, Formentera, Ibiza) and Canary (Tenerife) Islands (Table 2). It is another polyphagous species, although nearly all of its known hosts are gall-formers. It has been previously recorded in the region as a parasitoid in galls of the cynipids *Isocolus lichtensteini* (Mayr) on *Centaurea* (Lleida, Majorca) and *Plagiotrochus quercusilicis* (Fabricius) sex. gen. on *Quercus* (Madrid), the tephritids *Myopites* sp (p.) on *Inula* (Girona, Majorca) and *Bactrocera oleae* (Rossi) (Diptera, Tephritidae) on *Olea* (Barcelona), the cecidomyiids *Stefaniella atriplicis* (Kieffer) and *Stefaniola salsolae* (Tavares) (Diptera, Cecidomyiidae) on *Atriplex* (Zaragoza, Huesca and Lleida in Spain, Albufeira in Portugal), *Lasioptera eryngii* (Vallot) on *Eryngium* (Lleida, Albufeira (Portugal) and unidentified cecidomyiid galls on *Artemisia* (Murcia). *Eupelmus (M.) muellneri* was, in addition, reared in Lleida by A. Ribes from two species of cecidogenic Lepidoptera: *Coleophora cf serinipennella* Christoph (Coleophoridae) on *Atriplex* and, at two sites, *Parapodia sinaica* (Frauenfeld) (Gelechiidae) on *Tamarix* (Askew & Nieves-Aldrey, 2000, 2017; Fusu, 2017). A newly reported host is the cynipid *Diplolepis nervosa* (Curtis) on *Rosa*, 2♀ emerging from galls collected in Lleida (Torres de Segre) in 2012, RRA; the single Spanish specimen of *E. (M.) muellneri* noted in Askew *et al.*, 2006:34 from unidentified smooth pea galls of *Diplolepis* sp. probably had the same host species. In addition to these gall-forming hosts, *E. (M.) muellneri* is reported to have been associated with unnamed Scolytidae (Coleoptera) on *Euphorbia* in Tenerife (Fusu, 2017:84).

Eupelmus (M.) muellneri has been found in the field in Madrid, Barcelona, Girona (Tossa de Mar) Zarago-

Table 1.— Numbers of *Eupelmus (Macroneura)* in samples collected in a Malaise trap at La Parata, Mojácar (Almería) in 2013.

Tabla 1. Número de ejemplares, desglosados por períodos de muestreo, de las especies de *Eupelmus (Macroneura)* colectadas con una trampa Malaise en La Parata (Mojácar, Almería) que se mantuvo operativa desde mayo hasta agosto de 2013.

	2-13.v	13.v-24.vi	24.vi-1.vii	21.vii-viii	3-28.viii	Subt.♂♀	Totals
<i>E. aseculatus</i>	♀ 3	14	9	8	3	37	37
<i>E. maculatus</i>	♀ 1	-	-	-	-	1	1
<i>E. muellneri</i>	♀ 4	5	1	2	-	12	156
	♂ 41	44	43	15	1	144	
<i>E. seculatus</i>	♀ 1	-	1	3	-	5	33
	♂ 6	18	1	3	-	28	
<i>E. barai</i>	♀ -	1	-	-	-	1	91
	♂ 2	61	22	4	1	90	
<i>E. messene</i>	♀ 2	27	2	9	-	40	40
Totals	60	170	79	44	5	358	358

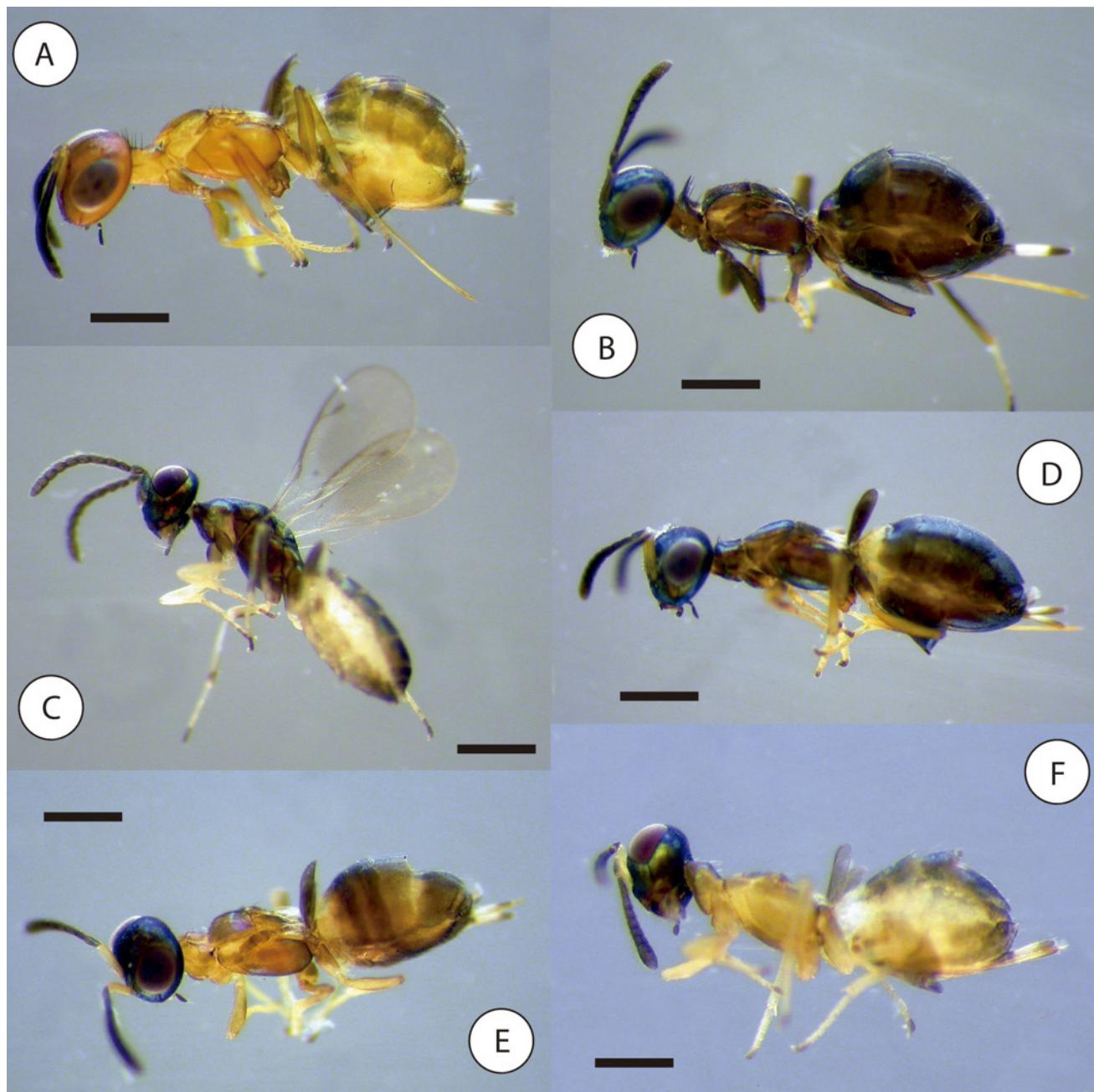


Fig. 2.—Habitus of selected species of *Eupelmus (Macroneura)*: (A) *Eupelmus (Macroneura) aseculatus* Kalina, female. (B) *Eupelmus (Macroneura) muellneri* Ruschka, female (C) *Eupelmus (Macroneura) vesicularis* (Retzius), male. (D) *Eupelmus (Macroneura) vesicularis* (Retzius), female. (E) *Eupelmus (Macroneura) seculatus* (Ferrière), female. (F) *Eupelmus (Macroneura) messene* Walker, female. Scale bar 0.5 mm.

Fig. 2.—Habitus de especies seleccionadas de *Eupelmus (Macroneura)*: (A) *Eupelmus (Macroneura) aseculatus* Kalina, hembra. (B) *Eupelmus (Macroneura) muellneri* Ruschka, hembra. (C) *Eupelmus (Macroneura) vesicularis* (Retzius), macho. (D) *Eupelmus (Macroneura) vesicularis* (Retzius), hembra. (E) *Eupelmus (Macroneura) seculatus* (Ferrière), hembra. (F) *Eupelmus (Macroneura) messene* Walker, hembra. Barra de escala 0.5 mm.

za (Pina de Ebro), Lleida (Torres de Segre), Alicante (Torrevieja), Granada (Calahonda), Murcia (Fortuna), Málaga, Castellón, Valencia and Almería, and it was the most abundant species in samples collected in a Malaise trap operated in the last named province at Mojácar (La Parata) (Table 1).

Eupelmus (Macroneura) seculatus (Ferrière, 1954) (Fig. 2E)

A species with a western Mediterranean range that is quite widespread in Spain including the Balearic Islands (Ibiza, Cabrera), and it is present in the Canary

Table 2.— Records of species of *Eupelmus (Macroneura)* in Peninsular Spain and Portugal, Balearic and Macaronesian Islands.Tabla 2.— Especies citadas de *Eupelmus (Macroneura)* de España penínsular, Portugal, Islas Baleares y Macaronesia (Islas Canarias, Azores y Madeira).

	Continental Portugal	Continental Spain	Balearic Islands	Canary Islands	Madeira	Azores
<i>E. aseculatus</i>	-	*	-	-	-	-
<i>E. falcatus</i>	-	*	-	-	-	-
<i>E. maculatus</i>	-	*	-	-	-	-
<i>E. muellneri</i>	*	*	*	*	-	-
<i>E. seculatus</i>	-	*	*	*	-	-
<i>E. barai</i>	-	*	*	-	*	-
<i>E. messene</i>	*	*	-	-	*	*
<i>E. vesicularis</i>	*	*	-	-	-	-

Islands but has not yet been reported from Portugal (Table 2). The record from the Canary Islands is new: La Gomera, Antoncojo, 26.iii.1979, RRA. It is polyphagous, but has been cited mainly as a parasitoid in galls of Cecidomyiidae and Cynipidae. In Spain 5♀♀ and 2♂♂ have been reared, the male described for the first time, from an unidentified cecidomyiid gall in *Ononis* flowers (Pujade-Villar, 1989), and also from galls of species of Cecidomyiidae on *Artemisia* (*Rhopalomyia baccarum* (Wachtl), Askew & Nieves-Aldrey, 2000), *Salsola* (*Stefaniola salsolae*, Fusu, 2017 and Askew & Nieves-Aldrey, 2017) and *Eryngium* (*Lasioptera eryngii*, Fusu, 2017). Emergence from galls of an unidentified cecidomyiid in seed heads of *Salvia lavandulifolia* (Madrid, Arganda, galls collected xi.2002, 1♀ emerged 2003, RRA) constitutes a new host record. Cynipid host galls in Spain are those of two species of *Plagiotrochus*, *P. quercusilicis* and *P. australis* on evergreen *Quercus* (Askew & Nieves-Aldrey, 2004), *Aulacidea laurae* Nieves-Aldrey on *Scorzonera (Podospermum) laciniata* (Askew et al., 2006), *Timaspis lampsanae* Perris on *Lapsana* (Askew et al., 2006), and *Xestophanes potentillae* (Retzius) on *Potentilla* (Askew et al., 2006).

Eupelmus (M.) seculatus has been found in the region in Catalonia, Zaragoza (Pina de Ebro), Lleida (Trempl), Madrid (El Escorial), Jaén, Castellón (Benicasim), Valencia, Ciudad Real, and at Mojácar (La Parata) in Almería where a Malaise trap was operated (Table 1).

THE *EUPELMUS VESICULARIS* COMPLEX

Eupelmus (Macroneura) barai (Fusu, 2017)

This species is the ‘dark form’ (Fusu, 2010) in the *E. vesicularis* aggregate. It is distributed across central and southern Europe and its occurrence in Spain as a parasitoid in galls of Cynipidae galling *Quercus* (*Andricus quercusradicis* sex. gen., *Callirhytis glandium* asex. gen., *Cynips divisa* Hartig asex. gen., *Neuroterus albipes* (Schenck) sex. gen., *Trigonaspis bru-*

neicornis Kieffer asex. gen. and *T. mendesi* Tavares asex. gen.) is previously recorded (Askew & Nieves-Aldrey, 2017, Fusu, 2017). Some Spanish specimens reared by JLN-A from galls of *A. quercusradicis* (1♀), *C. glandium* (1♀) and *C. divisa* (11♀♀, 8♂♂) are made paratypes by Fusu. A single male which emerged from a gall of the cynipid *Plagiotrochus quercusilicis* on *Quercus ilex*, collected in Zaragoza (Pina de Ebro) in 1996 by J. Blasco-Zumeta, is reported as ‘*Eupelmus vesicularis*’ (Askew et al., 2001).

Eupelmus (M.) barai, in addition to being a parasitoid in cynipid oak galls, is well represented in the parasitoid fauna of galls of Cynipidae and Cecidomyiidae on herbaceous plants and shrubs. It has been reared by JLN-A from galls of the cynipids *Timaspis phoenixopodus* Mayr on *Lactuca* (Madrid, 1984) (Askew et al., 2006 - as ‘*Eupelmus vesicularis*’, Fusu, 2017), and *Liposthenes kernerii* (Wachtl) on *Nepeta* (Madrid, 2 localities, 1989, JLN-A), Fusu (2017) designating as paratypes 2♀♀ from the host galls of the latter. The records of ‘*Eupelmus vesicularis*’ reared in mainland Spain from galls of the cynipids *Phanacis caulincola* (Hedicke), *P. centaureae* Förster and *Timaspis lampsanae* (Askew et al., 2006), and probably that of *Dias-trophus rubi* (Bouché) (Pujade-Villar, 1992), refer to *E. (M.) barai*. The specific identity of the *Macroneura* referred to as ‘*Eupelmus vesicularis*’ (Askew et al., 2006), reared from the galls of *Aulacidea tragopogonis* (Thomson), *Xestophanes potentillae* and *Diplolepis mayri* (Schlechtendal), is very probably *E. (M.) barai*, but this needs to be confirmed. Stems of *Cichorium intybus* from Lleida (Trempl, 2010, RRA) yielded 2♂♂, presumed parasitoids of the cynipid *Timaspis cichorii* (Kieffer) or its associates (further material of both sexes with the same data was reared by A. Ribes. Stems of *Centaurea* from Madrid (Gascones) collected v.2004 produced, a month later, 4♀♀ and 5♂♂ *E. barai*, and also females of *E. (M.) messene* (hosts not known but probably *Phanacis centaureae* or associates). Galls of *Phanacis hypocoeridis* (Kieffer) from Madrid (Colmenar Viejo, San Pedro), collected RRA xii.2005, yielded 2♂♂ *E. (M.) barai* in v.2006

together with *Eupelmus atropurpureus* Dalman. An unidentified cynipid gall on *Hieracium* from Formentera (San Fernando, 1988, M. Boness) produced a single male *E. (M.) barai*.

Cecidomyiid host gall records from the region concern *Rhopalomyia baccarum* on *Artemisia campestris*, 2♂♂ emerging from a sample of these galls collected Zaragoza, Los Monegros, 1996 (Askew et al., 2001), and *Lasioptera eryngii* (Lleida, 2 localities, 2007, A. Ribes), 2♂♂ being paratypes (Fusu, 2017).

Fusu (2017) also includes in his type material non-reared females collected by Z. Bouček in Barcelona (1971), Santander (1973) and Madrid (1974). The record of '*Eupelmella vesicularis*' from Majorca (Askew, 1975) refers to *E. (M.) barai*, as probably does that of Graham (1979) for Madeira (Table 2).

An exceptional record is of 1♀ emerging from a pupa of the nymphaline butterfly *Euphydryas aurinia* (Rottemburg); the host was laboratory reared and placed in the field as a prepupa, (2006, Barcelona (Sallent), C. Stefanescu & J. Planas). It is not known whether or not the eupelmid was behaving as a secondary parasitoid.

Specimens of *E. barai* have been caught in the field at the following localities additional to those mentioned above: Majorca (La Albufera), Girona (Tossa de Mar), Soria (Abejar) and Castellón, and numbers found in a Malaise trap at La Parata (Almería) are included in Table 1.

Eupelmus (Macroneura) messene (Walker, 1839) (Fig. 2F)

Eupelmus (M.) messene was described by Francis Walker from New Zealand and recognised as belonging to the *E. (M.) vesicularis* complex in Fusu's (2017) excellent study. It is the 'light form' in the aggregate (Fusu, 2010) and is plentiful in south-western Europe, but only females are known. It is almost certainly thelytokous (Fusu, 2017). The hosts listed for *E. (M.) messene* by Fusu (2017) are in the four major endopterygote orders and it is undoubtedly a highly polyphagous parasitoid, although most hosts are endophytic in plant stems or galls.

In the region, *E. (M.) messene* is recorded by Fusu (2017: 74,75) from Portugal (including Madeira and the Azores) and Spain, although it is not yet reported from the Canary Islands (Table 2). However, Iberian host records are surprisingly scarce and to date we can present only the rearing of 1♀ from cecidomyiid galls in fruits of *Halimione portulacoides* in Portugal (Algarve, Ferraguda, 1999, M. Boness) and an emergence of 10♀♀ from the collection of *Centaurea* stems (Madrid, Gascones, v.2004, RRA) that also yielded *E. (M.) barai* (see above) (no host was detected although the stems probably contained galls of the cynipid *Phanacis centaureae*). One of these specimens of *E. (M.) messene* from *Centaurea* stems was identified by Fusu (2017: 77). Field captures cited by Fusu (2017) are from Lleida and Catalonia in Spain, Porto in Portugal,

from Santa Maria in the Azores, and from Garajau and Faja da Nogueira in Madeira. The species seems to be quite plentiful in Madeira where additional sites are Curral das Freiras, Machico, Boca do Risco and São Jorge (1981, RRA). Material in samples from the Malaise trap at La Parata (Almería) is detailed in Table 1.

Eupelmus (Macroneura) vesicularis (Retzius, 1783) (Figs 2C, 2D)

This is the third species in the *E. (M.) vesicularis* complex which is known to occur in the region studied, and it is the least common. It has a rather north-easterly range and is, with the exception of one uncertain record, the only species in the complex that occurs in the British Isles (Fusu, 2017). Fusu suggests that it seems to have a preference for a more humid and cooler climate and is often montane. We have found *E. (M.) vesicularis* not uncommonly in the French Pyrénées, but only at a few places on the Spanish side of the mountains, and on the north coast of Spain. However, there are also somewhat discordant, more southerly elements, in the distribution pattern.

Fusu (2017: 83) gives a single record from Spain (1♀ Cantabria, Castro Urdiales, 1973, Z. Bouček). We have found specimens in Lleida (Bossost, 1♂ and Vall d'Arán, 1♀, both 1995, RRA), Huesca (Jaca, 1♀, 1973, RRA) and Gipuzkoa (Orio, 2♀♀, ix.1994, RRA). A new national record appears to be 1♀ from Portugal (Monte Gordo, Algarve, on *Retama* flowers, 14.iii.1999, M. Boness) (Table 2). This specimen was originally determined as *E. (M.) barai*, but it lacks any indication of violet colouration on the mesoscutum. *Eupelmus (M.) vesicularis* was not found in the La Parata Malaise trap samples.

The only known reared specimens from the region are 3♂♂ which emerged iii.2019 from galls of the cynipid *Andricus crispator* Tschek collected 8.ii.2019 from *Quercus suber* in Málaga province (Pujerra, JLN-A & D. Gil-Tapetado). The galls were collected in the oak forests of the Sierra Bermeja, south of Pujerra, at an altitude of about 700m. These specimens differ slightly in the form of their funicle segments from males of *E. (M.) vesicularis* collected in France and England, and their specific identity requires verification. Three other specimens of '*Eupelmus vesicularis*' were recorded as parasitoids in galls of *A. crispator* Tschek collected in Hungary (Askew et al., 2013), but this material is not available for re-examination.

Discussion

EUPELMUS (MACRONEURA) IN THE LA PARATA MALAISE TRAP SAMPLES

A total of 358 *Macroneura* was found in the trap samples. These were attributed to six species (Table 1), but *E. (M.) maculatus* was represented by just a

single female. There were about 2.7× as many males as females, even though males are not known for three of the six species. This numerical male bias is because males are fully winged whilst females are brachypterous, and a Malaise trap captures mostly insects which are intercepted in flight.

The most abundant species in the samples was *E. (M.) muellneri* (43.5%) although the thelytokous *E. (M.) messene* and possibly thelytokous *E. (M.) aseculatus* were surprisingly well-represented, outnumbering the females of those species which are known to have both sexes.

Acknowledgements

Financial support of RRA at the Museo Nacional de Ciencias Naturales (CSIC) in Madrid was provided by the European Community's Programme 'Research Infrastructure Action' under SYNTHESYS (ES-TAF-4868). JLNA was supported in part by research projects (MINECO/FEDER, UE) CGL2015-66571-P, (AEI/FEDER, UE) AGL2016-76262-R and Encomienda de Gestión del MAPAMA a la Agencia Estatal CSIC, exp. 16MNES003.

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