



## New data on the Iberian endemic bee genus *Flavipanurgus* Warncke (Hymenoptera: Apoidea: Andrenidae): Ecological and genomic data reveal a hidden species

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### Abstract

*Flavipanurgus* is a small genus of panurgine bees known only from the Iberian Peninsula. Despite its status as one of the few bee genera endemic to Europe, *Flavipanurgus* are poorly represented in collections and until recently, their ecology had been almost unknown. *Flavipanurgus ibericus* (Warncke, 1972) was described from southern Iberia, with a northern subspecies *F. i. kastiliensis* (Warncke, 1987) later described from the north. Recent collections in Portugal have revealed clear differences in the pollen collecting patterns of the two taxa, with southern females collecting exclusively from *Jasione montana* and northern females from *Sedum* species. In combination with this ecological difference, COI and 28S barcode data indicate that *Flavipanurgus kastiliensis* **stat. nov.** should be raised to full species status. The male of *Flavipanurgus ibericus* s. str. is described for the first time, and updated keys to *Flavipanurgus* species are provided. *Flavipanurgus fuzetus* Patiny, 1999 is recorded for the first time from Spain. Further significant records and new floral associations for *Flavipanurgus* are also presented.

**Key words:** DNA barcoding, host plant choice, identification key, oligolecty, taxonomy

### Introduction

*Flavipanurgus* (Panurginae: Panurgini) was first proposed by Warncke (1972) as a subgenus of *Panurgus* but this was raised to genus level by Patiny (1999a). All known species are endemic to the Iberian Peninsula and appear to be pronounced floral specialists, with species specialising on flowers from the botanical families Caryophyllaceae, Cistaceae and Crassulaceae (González-Varo *et al.* 2016; Wood & Cross 2017).

*Flavipanurgus* are small black bees with white to yellow markings on the head, mesosoma and metasoma. In Iberia, *Flavipanurgus* species can be separated from similarly yellow-marked species of *Camptopoeum* (*Camptopoeum*) Spinola by the former's relatively short tongues that are approximately only twice as long as broad. Males can be separated from *Simpanurgus phyllopodus* (Warncke, 1972) as the former lack the distinctive flattened and elongate front tarsi and the clavate and flattened flagellum of the latter. Female material of *S. phyllopodus* is unknown.

*Flavipanurgus ibericus* was first described by Warncke (1972) based on female specimens from Toledo in central Spain and Dogueno, in southern Portugal. Later, Warncke (1987) recognized the subspecies *kastiliensis* based on material from the Sistema Central, south of Salamanca in Spain. Though material was available to describe the male of *kastiliensis*, the male of the nominate form, *ibericus*, remained unknown.

In May 2017, *F. ibericus ibericus* was discovered to be locally numerous at a site in southern Portugal near Mértola only 26 km east of the original Portuguese location. Both sexes were present, including several mating pairs (Figure 1). The opportunity was taken to take samples of the males and make observations of the foraging behaviour. In striking contrast to the behaviour of *F. ibericus kastiliensis*, an oligolecte of *Sedum* (Wood & Cross

2017, as *F. ibericus*), *F. ibericus ibericus* was found to collect pollen exclusively from *Jasione montana* L. This divergent pattern of pollen collection in a subfamily known for its high proportion of oligolectic species (Rozen 1967) suggested the presence of an additional species within *F. ibericus*.

In this paper, we present the first genomic data from *Flavipanurgus* species and review the available data on distribution, ecology and pollen foraging behaviour for the genus. Based on this ecological and genomic data, we propose elevating *F. kastiliensis* **stat. nov.** to species rank. We present a description of the male of *F. ibericus* sensu stricto along with an updated key to the genus. We also take the opportunity to add significant new distribution data and floral associations for the other species of *Flavipanurgus*.

## Material and methods

Fresh *Flavipanurgus* material was available from four species of *Flavipanurgus* (Table 1). A single mid leg was removed and DNA was extracted using the DNeasy blood and tissue kit protocol (Qiagen). Both cytochrome c oxidase subunit 1 (COI) and 28S ribosomal DNA were amplified. Initially LepF1 and LepR1 (Herbert *et al.* 2004) were used to amplify COI but amplification repeatedly failed for a majority of samples. Samples were re-run using the internal primer pair LepR1 and MLepF1 (Hajibabaei *et al.* 2006). Primers D2-3-F and D2-3-R (Smith & Brown 2008) were used to amplify 28S. PCR and sequencing reactions followed standard protocols (Hajibabaei *et al.* 2005). Sequences were aligned using MEGA X (Kumar *et al.* 2018) and were uploaded to GenBank (Table 1).

For the description of the male of *F. ibericus*, terminology follows Michener (2007). Field observations of *Flavipanurgus* general behaviour and pollen preferences were made in situ, with photographs taken where possible. These records of pollen hosts are based on direct observation of foraging behaviour in the field and for *F. kastiliensis* on the microscopic analysis of pollen loads (Wood & Cross 2017). For field observations, care was taken to ensure that either pollen gathering behaviour or the colour of collected loads of female bees laden with pollen were recorded. The nomenclature used is from Flora-On (2014).

**TABLE 1.** Specimen information and GenBank accession numbers for *Flavipanurgus* material used in this study.

Species	Date	Country	Locality	Latitude	Longitude	COI	28S
<i>Flavipanurgus flavus</i> (Erichson)	9 May 2016	Portugal	Aljezur	37.314	-8.872	MH686507	MH699075
<i>Flavipanurgus flavus</i> (Erichson)	9 May 2016	Portugal	Aljezur	37.314	-8.872	MH686508	MH699076
<i>Flavipanurgus fuzetus</i> Patiny	27 April 2016	Portugal	Cacela Velha	37.157	-7.544	MH686509	MH699077
<i>Flavipanurgus ibericus</i> (Warncke)	7 May 2017	Portugal	Mértola	37.557	-7.770	MH686510	MH699078
<i>Flavipanurgus ibericus</i> (Warncke)	7 May 2017	Portugal	Mértola	37.557	-7.770	MH686511	MH699079
<i>Flavipanurgus kastiliensis</i> (Warncke)	28 June 2016	Portugal	Pardelhas, Vila Real	41.336	-7.864	MH686512	MH699080
<i>Flavipanurgus kastiliensis</i> (Warncke)	28 June 2016	Portugal	Pardelhas, Vila Real	41.336	-7.864	MH686513	MH699081
<i>Flavipanurgus kastiliensis</i> (Warncke)	30 June 2016	Portugal	Serra de Montesinho, Bragança	41.952	-6.764	MH686514	MH699082

## Results

Both COI and 28S sequences were successfully amplified from all specimens. No ambiguous base calls were detected. Use of the internal primer pair generated COI sequences 437 base pairs in length. Species were well differentiated by these sequences (Table 2) with interspecific divergence of between 8.2–12.4% and intraspecific

divergence of between 0.0–0.5%, well over the suggested threshold of 2% divergence likely to indicate separate species (Schmidt *et al.* 2015).

Generated 28S sequences were around 750 base pairs in length. Sequences from putative species were identical (Table 3). Interspecific divergence varied between and 0.4–2.2%, with *F. ibericus* and *F. kastiliensis* varying by 0.9%.

**TABLE 2.** Percentage distance scores between COI barcodes across *Flavipanurgus* specimens.

	<i>Flavipanurgus flavus</i>	<i>Flavipanurgus flavus</i>	<i>Flavipanurgus fuzetus</i>	<i>Flavipanurgus ibericus</i>	<i>Flavipanurgus ibericus</i>	<i>Flavipanurgus kastiliensis</i>	<i>Flavipanurgus kastiliensis</i>	<i>Flavipanurgus kastiliensis</i>
<i>Flavipanurgus flavus</i>								
<i>Flavipanurgus flavus</i>	0.2							
<i>Flavipanurgus fuzetus</i>	12.4	12.1						
<i>Flavipanurgus ibericus</i>	9.2	8.9	12.4					
<i>Flavipanurgus ibericus</i>	8.9	8.7	12.1	0.2				
<i>Flavipanurgus kastiliensis</i>	8.5	8.2	12.4	9.6	9.4			
<i>Flavipanurgus kastiliensis</i>	8.5	8.2	12.4	9.6	9.4	0.0		
<i>Flavipanurgus kastiliensis</i>	8.5	8.2	12.4	9.6	9.4	0.5	0.5	

**TABLE 3.** Base pair substitution differences for *Flavipanurgus* species for nuclear 28S ribosomal DNA (~750 bp).

	146	152	160	161	171	176	178	212	274	299	307	372	374
<i>Flavipanurgus flavus</i>	G	T	T	T	G		A	T	C	C	C	C	C
<i>Flavipanurgus flavus</i>	G	T	T	T	G		A	T	C	C	C	C	C
<i>Flavipanurgus fuzetus</i>	G	C	T	T			G	A	C	T	T		G
<i>Flavipanurgus ibericus</i>	G	T	T	T			A	T	T	C	C	C	C
<i>Flavipanurgus ibericus</i>	G	T	T	T			A	T	T	C	C	C	C
<i>Flavipanurgus kastiliensis</i>	A	C	C	C		A	A	T	T	C	C	C	C
<i>Flavipanurgus kastiliensis</i>	A	C	C	C		A	A	T	T	C	C	C	C
<i>Flavipanurgus kastiliensis</i>	A	C	C	C		A	A	T	T	C	C	C	C
	380	385	395	425	426	430	448	480	599	630	652	669	
<i>Flavipanurgus flavus</i>	T	C	A			T	C	G	C	G	A	A	
<i>Flavipanurgus flavus</i>	T	C	A			T	C	G	C	G	A	A	
<i>Flavipanurgus fuzetus</i>		T	A	C	T	C	C	G	T	G	G	A	
<i>Flavipanurgus ibericus</i>	T	C	G			T	C	A	C	G	A	A	
<i>Flavipanurgus ibericus</i>	T	C	G			T	C	A	C	G	A	A	
<i>Flavipanurgus kastiliensis</i>	T	C	G			T	T	G	C	A	A		
<i>Flavipanurgus kastiliensis</i>	T	C	G			T	T	G	C	A	A		
<i>Flavipanurgus kastiliensis</i>	T	C	G			T	T	G	C	A	A		

### Description of the male of *Flavipanurgus ibericus* (Warncke)

**Material examined:** PORTUGAL: São Sebastião dos Carros, 7.v.2017 5m# (leg. I.C. Cross). 1m# Deposited in

the Natural History Museum, London

Lat. 37° 30' 6", Long. 7° 41' 56" W.

**Diagnosis.** The white markings are of a variable extent and it is difficult to find consistent colour differences from *F. kastiliensis*. The white areas of the face and scutellum tend to be less extensive in *F. ibericus* (Table 4), and the inner surface of the hind tibia is consistently marked with black (Figure 8). Unlike many Portuguese *F. kastiliensis*, the white spot on the frons is not joined to the supraclypeal area by a narrow, white stripe. However, though a useful character, this is by no means a reliable indicator of identity. Two out of six Portuguese specimens and the single Spanish *F. kastiliensis* specimen available also lacked this stripe. The short white dash on the scutellum contrasts with northern Portuguese *F. kastiliensis* in which the scutellum has, at the very least, an extensive white “L”-shaped margin at the rear corners and is frequently almost entirely white. Overall, the ivory-white spots at the rear of terga 1–7 are slightly less extensive than in *F. kastiliensis* but to an equally variable extent, such that it is impossible to point to any consistent differences. The genitalia show no consistent differences from those of *F. kastiliensis*.

**TABLE 4.** Distinguishing features and variation in colour patterns of male *Flavipanurgus ibericus* and *Flavipanurgus kastiliensis*.

Feature	<i>Flavipanurgus ibericus</i> Portugal (n = 5)	<i>Flavipanurgus kastiliensis</i> Portugal (n = 6)	<i>Flavipanurgus kastiliensis</i> Spain (n = 1)
Frontal spot joined to supraclypeal spot	No	Usually (2 specimens have the spots separated)	No
Extent of pale marks on scutellum	2 short white “dashes” at the rear corners	Varies from continuous white margin at hind and rear edges to scutellum almost entirely white	2 tiny white dots
White mark at top of gena	A broad, smooth rectangular spot, roughly the length of flagellar segments 10–12	Absent (2 specimens) or, at most, a smaller, irregular, elongate mark just longer than flagellar segments 11–12	Tiny dot on one side only
Tibia	Yellow, with an oval black spot or streak on the hind face.	Entirely yellow.	Entirely yellow.

**Description.** Small (5 mm) black bee with ivory-white and yellow markings (Figure 2). *Head:* Face (Figure 6) almost entirely pale in lower half; with clypeus, supraclypeal area, two small patches beneath antennal insertions and entire paraocular area to just above antennal insertions, white. Frons with small, central, white spot, halfway between middle ocellus and antennal insertions. Occasionally with small white spot just behind compound eye, at bottom of gena. Top of gena with large, rectangular spot. Mandibles and ventral surface of antennae largely white. *Thorax:* Black apart from the following white markings: band on pronotal collar, broken medially; pronotal lobes; tegulae and entire metanotum. Scutellum with short white “dash” posterolaterally. Legs with pale markings yellow. All femora black, with yellow in distal quarter and in narrow strip ventrally. Tarsi yellow but becoming progressively more infuscated with dull brownish-black from fore tarsus to hind tarsus. All tibiae yellow with black oval spot or streak on hind face; least developed on fore tibia. *Metasoma:* Black, with ivory-white markings of variable extent along distal part of terga 1–7. Tergum 1 with two roundish spots apicolaterally. Occasionally (1 of 5) with two much smaller, submedial spots. Terga 2–6 with pair of white wedge-shaped markings, each broadly indented by round, black spot mid-way along their front margin. On T5 markings occasionally contiguous. In darkest specimens, wedges across all terga widely separated and black spot breaks through to rear margin forming line of four, roughly equally-spaced spots. T6 has four white spots apically, central pair usually united in short strip. In darker with single, central pair of triangular spots that may be weakly joined. Genitalia (Figure 11).

### The pollen hosts of *Flavipanurgus ibericus* and *F. kastiliensis*

All the specimens of *F. ibericus* observed at São Sebastião dos Carros were found on *Jasione montana*. All females (n = ca. 20) examined closely had the tibial scopa full of the characteristic purple pollen of *Jasione* (Figure 3).

Though there is only one pollen record for *F. ibericus* so far, it is likely that it represents part of a limited range of pollen choices, if not the sole host. In support of this, an earlier record of a flower visit has emerged in the form of a photograph taken in 2011. This also shows *F. ibericus* on *Jasione montana* (see new data below). Narrow oligolecty on *Jasione* is known in *Dufourea halictula* (Nylander, 1852) (Ebmer 1984), but to our knowledge it has not been reported from other Western Palearctic bee species. Species broadly oligolectic on Campanulaceae have been recorded utilising *Jasione* as a pollen source, such as *Hoplitis mitis* (Nylander, 1852) (Müller 2017) and *Lasioglossum costulatum* (Kriechbaumer, 1873) (T. Wood, unpublished data, P. Westrich *pers. comm.*), so it is possible that *F. ibericus* may also be broadly oligolectic on Campanulaceae. However, given that all other *Flavipanurgus* species for which data are available show close association with one particular genus, this situation is considered less likely.

*Flavipanurgus kastiliensis* were found on a wider range of flowers. In northern Portugal both males and females were found in numbers on *Spergularia* (Caryophyllaceae). However, these visits were purely for nectar and no evidence of pollen collection was recorded. When it came to collecting pollen only species of *Sedum* were used (Figure 4). These included *Sedum anglicum* Huds., *S. brevifolium* DC., *S. hirsutum* All. and *S. pedicellatum* Boiss. & Reut. In contrast to *Jasione*, *Sedum* pollen is creamy-white to brown in colouration. Some *Sedum* species were completely ignored, despite being numerous in the same locality and visited by other bees. These species included *S. amplexicaule* (Sibth & Sm.) DC.

At both the northern Portugal and Picos de Europa sites, a search was made for *F. ibericus* using *Jasione montana*, which was abundant at both localities and, indeed, can be found widely in northern Iberia. No evidence of use of this plant, either for nectar or as a pollen source, was found at either site. The use of *Sedum* as an exclusive pollen host by *F. kastiliensis* was consistent at sites 340 km apart on either side of the Spanish/Portuguese border. In a subfamily (Rozen 1967) and genus of strongly oligolectic or even monolectic bees (González-Varo *et al* 2016; Wood and Cross 2017), this difference in host plant use is significant.

Bee species showing minor or subtle morphological differences have been proposed and accepted on the basis of distributional, phenological and behavioural differences. The *Colletes succinctus* group contains three species in western Europe—*C. halophilus* Verhoeff, 1944, *C. hederarum* Schmidt and Westrich, 1993, and *C. succinctus* (Linnaeus, 1758). Morphologically, the three species are very difficult to identify, but each has a specific ecological requirement, broadly favouring coastal saltmarsh with *Tripolium pannonicum* (Jacq.) Dobroc., general habitats with *Hedera helix* L. and sandy habitats with Ericaceous plants respectively (Kuhlmann *et al.* 2007; Müller and Kuhlmann 2008). The species complex appears to be very young, with a small number of distinguishing substitutions in four studied genes (Kuhlmann *et al.* 2007). For *F. ibericus* and *F. kastiliensis*, there is marked sequence divergence between individuals presented here.

### New distribution data and floral records for *Flavipanurgus*:

Current knowledge on the distribution of *Flavipanurgus* species was summarised by Patiny (2012).

***Flavipanurgus flavus*** (Friese, 1897): PORTUGAL: Algarve, Faro, Corte do Gago, 21.iv.2011, 1m# (photo V. Jacinto, det. I.C. Cross) Lat. 37°17' N, Long. 7° 32' W. On *Cistus ladanifer*, a first post 2000 record for the eastern Algarve. SPAIN: Andalucía, Málaga, El Cielo, 30.iv.2018, 1m# (det. & leg. I.C. Cross) Lat. 36° 47' 23" N, Long. 3° 49' 30" W. On *Halimium umbellatum*, a new floral record for this species and the first post 2000 record for southern Spain. Specimen in I. Cross collection.

***Flavipanurgus fuzetus*** Patiny, 1999: Originally known only from its type locality at Fuzeta in southern Portugal until it was rediscovered in the eastern Algarve in 2016 (Wood & Cross 2017). The first record for Spain. As predicted in Wood & Cross 2017, this species was first recorded from coastal saltmarsh in Huelva province, Andalucía. As is typical of *F. fuzetus*, once discovered, males and females were found to be locally numerous on *Spergularia marina* and *Frankenia laevis*. The latter is only a nectar source.

Material examined. SPAIN: Andalucía, Huelva, Marismas del Odiel, 6.v.2018, 3m# 3f# (det. & leg. I.C. Cross) Lat. 37° 13' 2" N, Long. 7° 18' 48" W. Specimens in I. Cross collection.

***Flavipanurgus ibericus***: PORTUGAL: Algarve, Faro, Corte do Gago, 17.v.2011, 1m# (photo V. Jacinto, det. I.C. Cross) Lat. 37° 17' N, Long. 7° 32' W. On *Jasione montana*, this is the earliest record for the Algarve.

*Flavipanurgus kastiliensis*: PORTUGAL: Minho, Vila Nova de Famalicão, 2.6.2018, 1f# (photo J. Oliveira, det. T.J. Wood). Lat. 41° 25' N, Long. 8° 31' W. On *Sedum* spp.

## Updated key to the genus *Flavipanurgus*

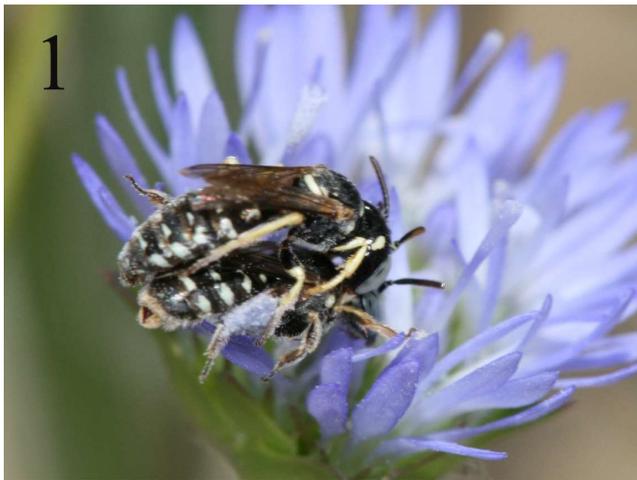
The most recent key to the genus *Flavipanurgus* is that of Warncke (1987). However, this deals only with the smaller species and doesn't take into account subsequent developments, such as the discovery of *F. fuzetus* Patiny 1999b, the discovery and description of its male (Wood & Cross 2017) and the proposed new status of *F. kastiliensis*. Therefore, as far as the males are concerned, Warncke's key only deals with three of the seven taxa. The key to females likewise deals only with three of the taxa, though characters to distinguish female *F. ibericus* and *F. kastiliensis* are given in the description of the latter. To overcome this growing deficit in the usefulness of the existing keys, new keys to the males and females of *Flavipanurgus* are therefore introduced here.

### Males

1. Larger species (forewing length > 5 mm) ..... 2
- Smaller species (forewing length < 4 mm) ..... 3
2. Yellow markings more pronounced. Abdomen with large, yellow, wedge-shaped spots on T1 to T5 up to a quarter the width of the tergites. Tegulae and pronotal lobes yellow-marked. .... *venustus* (Erichson, 1835)
- Yellow markings more restricted. Abdomen with at most small, lateral flecks. Tegulae and pronotal lobes black ..... *flavus* (Friese, 1897)
3. Facial markings ivory-white. Vertex and propodeum shagreened, matt. .... 4
- Facial markings yellow. Vertex and propodeum smooth and shiny ..... 6
4. Facial markings extensive. Paraocular area to antennal insertions white ..... 5
- Facial markings more restricted. Paraocular area with at most a small white square beneath antennal insertion ..... *fuzetus* Patiny, 1999
5. Metatibia entirely yellow (Figure 7). Supraclypeal area with white reaching top of antennal insertion. It is frequently joined by a pale, central strip to an elongate white spot on the frons below the middle ocellus (Figure 5). This strip is sometimes narrowly broken, in which case the gap is less than the height of the supraclypeal marking ..... *kastiliensis* (Warncke, 1987)
- Metatibia with a small, black oval spot or streak on the hind face (Figure 8). Supraclypeal area with white reaching half way up antennal insertion. It is well separated from the spot below the middle ocellus, by roughly the height of the supraclypeal marking. (Figure 6) ..... *ibericus* (Warncke, 1972)
6. Mandibles regularly tapered. Vertex broad, as wide as three ocellar diameters. Frons with a transverse, oval, central yellow spot. Yellow bands on the tergites narrowed to slightly broken ..... *granadensis* (Warncke, 1987)
- Mandibles broadened in the apical half. Vertex narrower, as wide as two ocellar diameters. Frons black. Abdomen with only yellow spots on the sides. .... *merceti* (Vachal, 1910)

### Females

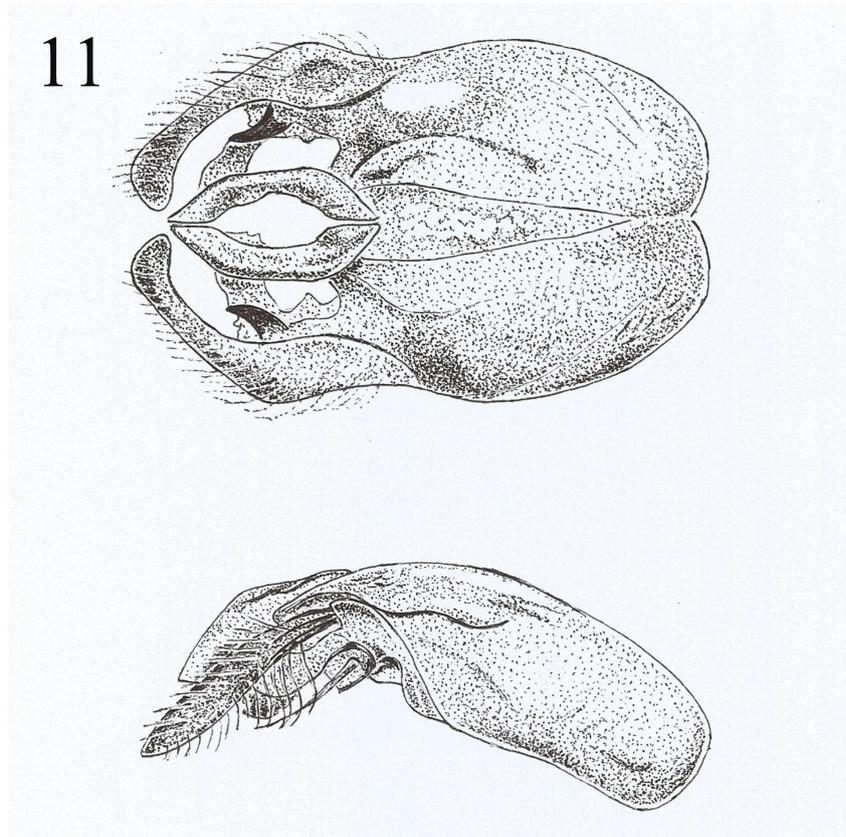
1. Larger species (forewing length > 5 mm) ..... 2
- Smaller species (forewing length < 4 mm) ..... 3
2. Face and metasoma with pronounced yellow markings ..... *venustus* (Erichson, 1835)
- Entire body black ..... *flavus* (Friese, 1897)
3. Abdomen extensively white-marked. T(2) 3–4 with ivory-white strips along the hind margin entire or only narrowly broken centrally. .... 4
- Abdomen mainly dark, with only a few, widely-separated, yellow spots. .... 6
4. Supraclypeal area white ..... 5
- Supraclypeal area black. .... *fuzetus* Patiny, 1999
5. Scutum more sparsely punctate, the punctures separated by twice the puncture diameter (Figure 9). Clypeus entirely black or, at most, with a narrow white line, slightly swollen in the middle, along the upper margin. This mark is less than half the area of the supraclypeal spot. No paraocular spots. .... *kastiliensis* (Warncke, 1987)
- Scutum more densely punctate, the punctures separated by roughly a puncture diameter (Figure 10). Clypeus white in a broad band along the upper margin, its width roughly a third of the height of the clypeus. This band is produced along the sides of the clypeus and has a central prominence below. Together, these form a broad, flattened trident at least the same area as the supraclypeal spot. Small white spots of variable extent on the paraocular area ..... *ibericus* (Warncke, 1972)
6. Metanotum almost completely punctate and matt, except for a narrow posterior region along the propodeum. T1 & 2 with a yellow spot on each side. T3 & 4 with an additional yellow spot each side of the middle. .... *granadensis* (Warncke, 1987)
- Propodeum dorsally smooth and shiny in an area as wide as the width of the metanotum. T1–3 with one small (reddish)-yellow spot at each side. .... *merceti* (Vachal, 1910)



**FIGURES 1–6.** 1: *Flavipanurgus ibericus* mating pair. 2: *Flavipanurgus ibericus* male habitus. 3: *Flavipanurgus ibericus* female with tibial scopa full of *Jasione* pollen. 4: *Flavipanurgus kastiliensis* female with tibial scopa full of *Sedum* pollen. 5: *Flavipanurgus kastiliensis* male face. 6: *Flavipanurgus ibericus* male face.

## Conclusions

Across all species, bees from the genus *Flavipanurgus* use pollens from the botanical families Campanulaceae, Caryophyllaceae, Cistaceae and Crassulaceae (González-Varo *et al* 2016, Wood & Cross 2017). The use of these diverse botanical families by *Flavipanurgus* further supports their generic status as distinct from *Panurgus* (Patiný 1999a), all members of which are oligoleges of Asteraceae (e.g. Rozen 1971; Westrich 1989).



**FIGURES 7–11.** 7: *Flavipanurgus kastiliensis* male dorso-lateral view showing hind tibia. 8: *Flavipanurgus ibericus* male dorso-lateral view showing hind tibia. 9: *Flavipanurgus kastiliensis* female scutum. 10: *Flavipanurgus ibericus* female scutum. 11: *Flavipanurgus ibericus* male genitalia, dorsal (above) and lateral (below) views.

The evolution of pollen host-plant choice in bees is incompletely understood. Closely related bees from the *Colletes succinctus* group utilise pollens of similar nutritive content. In contrast, bees in the *Melitta leporina* group utilise pollens without such compositional similarities, often from flowers with differing structures and symmetries (Vanderplank *et al.* 2017). The clear divergence in foraging choices between *Flavipanurgus* species using botanically unrelated, but morphologically similar, simple, radially symmetrical flowers appears to be closer to the trend observed in the *Melitta leporina* group, and offers an additional opportunity to assess these hypotheses regarding these behaviours in a different evolutionary lineage.

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## Literature

- Danforth, B.N., Cardinal, S., Praz, C., Almedia, E.A.B. & Michez, D. (2013) The impact of molecular data on our understanding of bee phylogeny and evolution. *Annual Review of Entomology*, 58, 57–78.  
<https://doi.org/10.1146/annurev-ento-120811-153633>
- Ebmer, A.W. (1984) Die westpaläarktischen Arten der Gattung *Dufourea* Lepeletier 1841 mit illustrierten Bestimmungstabellen (Insecta: Hymenoptera: Apoidea: Halictidae: Dufoureae). *Senckenbergiana biologica*, 4 (4/6), 313–379.
- Flora-On: Flora de Portugal Interactiva (2014) Sociedade Portuguesa de Botânica. Available from: <http://flora-on.pt/#/1> (accessed 1 August 2017)
- Hajibabaei, M., deWaard, J.R., Ivanova, N.V., Ratnasingham, S., Dooh, R.T., Kirk, S.L., Mackie, P.M & Hebert, P.D.N. (2005) Critical factors for assembling a high volume of DNA barcodes. *Philosophical Transactions of the Royal Society B*, 360, 1959–1967.  
<https://doi.org/10.1098/rstb.2005.1727>
- Hajibabaei, M., Smith, M.A., Janzen, D.H., Rodriguez, J.J., Whitfield, J.B. & Hebert, P.D.N. (2006) A minimalist barcode can identify a specimen whose DNA is degraded. *Molecular Ecology Notes*, 6, 959–964.  
<https://doi.org/10.1111/j.1471-8286.2006.01470.x>
- Hebert, P.D.N., Penton, E.H., Burns, J.M., Janzen, D.H., and Hallwachs, W. (2004) Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *Proceedings of the National Academy of Sciences*, 101, 14812–14817.  
<https://doi.org/10.1073/pnas.0406166101>
- Kuhlmann, M., Else, G.R., Dawson, A. and Quicke, D.L.J. (2007) Molecular, biogeographical and phenological evidence for the existence of three western European sibling species in the *Colletes succinctus* group (Hymenoptera: Apidae). *Organisms, Diversity & Evolution*, 7, 155–165.  
<https://doi.org/10.1016/j.ode.2006.04.001>
- Kumar, S., Stecher, G., Li, M., Knyaz, C. and Tamura, K. (2018) MEGA X: Molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution*, 35, 1547–1549.  
<https://doi.org/10.1093/molbev/msy096>
- Michener, C.D. (2007) *The Bees of the World*. 2<sup>nd</sup> Edition. John Hopkins University Press, Baltimore, 953 pp.
- Müller, A. (2017) Palaearctic Osmiine Bees. ETH Zurich, Available from: <http://blogs.ethz.ch/osmiini> (accessed 1 August 2018)
- Patiny, S. (1999a) Etude phylogénétique des Panurginae de l'ancien monde (Hymenoptera, Andrenidae). *Linzer Biologische Beiträge*, 31, 249–275.
- Patiny, S. (1999b) Description d'une nouvelle espèce de *Flavipanurgus* Warncke, 1972 (Hymenoptera, Andrenidae, Panurginae). *Notes fauniques de Gembloux*, 37 57–61
- Patiny, S. (2012) Atlas of the European Bees: genus *Flavipanurgus*. STEP Project, Atlas Hymenoptera, Mons, Gembloux. Available from: <http://www.zoologie.umh.ac.be/hymenoptera/page.asp?ID=24> (accessed 1 August 2018)
- Rozen Junior, J.G. (1967) Review of the biology of panurgine bees, with observations on North American forms (Hymenoptera: Apoidea). *American Museum Novitates*, 2297, 1–44.
- Rozen Junior, J.G. (1971) Biology and immature stages of Moroccan panurgine bees (Hymenoptera: Apoidea). *American Museum Novitates*, 2457, 1–37.

- Schmidt, S., Schmid-Egger, C., Morinière, J., Haszprunar, G. & Herbert, P.D.N. (2015) DNA barcoding largely supports 250 years of classical taxonomy: identifications for Central European bees (Hymenoptera: Apoidea partim). *Molecular Ecology Resources*, 15, 985–1000.  
<https://doi.org/10.1111/1755-0998>
- Smith, P.T. & Brown, B.V. (2008) Utility of DNA sequences for inferring phylogenetic relationships and associating morphologically dissimilar males and females of the bee-killing flies, genus *Melaloncha* (Diptera: Phoridae). *Annals of the Entomological Society of America*, 101, 713–721.  
<https://doi.org/10.1093/aesa/101.4.713>
- Vanderplank, M., Vereecken, N.J., Grumiau, L., Esposito, F., Lognay, G., Wattiez, R. & Michez, D. (2017) The importance of pollen chemistry in evolutionary host shifts of bees. *Scientific Reports*, 7, 43058.  
<https://doi.org/10.1038/srep43058>
- Warncke, K. (1972) Westpaläarktische Bienen der Unterfamilie Panurginae (Hym., Apidae). *Polskie Pismo Entomologiczne*, 52, 53–108.
- Warncke, K. (1987) Ergänzende Untersuchungen an den Bienen der Gattungen *Panurgus* und *Melitturga/Andreninae*, Apidae, vor allem dem türkischen Raum. *Bolletino del Museo Civico di Storia Naturale di Venezia*, 36, 75–107.
- Westrich, P. (1989) *Die Wildbienen Baden-Württembergs*. Eugen Ulmer, Stuttgart, 972 pp.
- Wood, T.J. & Cross, I. (2017) *Camptopoeum* (*Camptopoeum*) *baldocki* spec. nov., a new panurgine bee species from Portugal and a description of the male of *Flavipanurgus fuzetus* Patiny (Andrenidae: Panurginae). *Zootaxa*, 4254 (2), 285–293.  
<https://doi.org/10.11646/zootaxa.4254.2>